

No. 5 — *On Some Burmese Earthworms of the Moniligastrid Genus Drawida*¹

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INTRODUCTION

This contribution completes publication of results of the author's study of Burmese moniligastrids. Specimens listed herein, with few exceptions, were collected between 1932 and the end of 1941 when the survey was finally terminated by the Japanese invasion. Locality lists for the period subsequent to 1932 probably are complete for most of the species considered below, though information about certain anatomical and other matters

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is available no longer. Some comparable data for one species was obtained recently, through assistance of Dr. H. K. Bhatti, from a Pakistani series. Unpublished records of other Burmese drawidas were destroyed along with the specimens during World War II.

The Burma survey provided, for the first time, considerable material of moniligastrid species. The variation, both individual and geographic, that was revealed required consideration (p. 308) of the usefulness to taxonomy of various characters. In addition to the taxonomic accounts, discussions of anatomy (pp. 299 and 305) provide the foundation for a first attempt at a phylogeny of the family (p. 355), as well as for discussion of certain assumptions basic in classical phylogenies. An "ingenious" contraction theory, the only previous attempt to bridge the gap between moniligastrids and other megadriles, is critically examined for the first time (p. 363), and other ways in which early oligochaete evolution may have proceeded are suggested.

SYSTEMATICS

OLIGOCHAETA, Class or Order

The lower rank was acceptable to classical authorities, Beddard (1895), Michaelsen (1900, 1921, 1928-1930) and Stephenson (1923, 1930). The order, along with the Polychaeta, long was included in a class Chaetopoda. Since 1900, oligochaetes have been found to be more closely related to the leeches than to the polychaetes. Michaelsen's *Acanthobdellidae*, in Kükenthal and Krumbach's massive "Handbuch der Zoologie," is in the Oligochaeta and also in the Hirudinea! To show the relationship, some authorities, including Stephenson (1930), place the leeches also in the Chaetopoda. Michaelsen, however, erected for the two more closely related orders the class Clitellata which has not been generally accepted. *Acanthobdella* was retained in the Oligochaeta by Pickford (1948) and Yamaguchi (1953) but was excluded by Stephenson (1930) and Avel (1959). Though "The great gulf in intra-annelidan phylogeny is that which divides the polychaetes from the oligochaetes" Pickford (1948) believed that convenience required the three main annelidan groups to have equal rank as classes. If a classification is to indicate the closer leech-oligochaete relationship, some place presumably ought to be found for the Clitellata.

Between order and families, in his later systems Michaelsen interposed two (1921), then three (1928), and finally four (1930)

suborders as well as various series. These taxa were accepted by Pickford, Yamaguchi and Avel though with some modifications, including raising suborders (Pickford, Avel) to ordinal rank. This elaboration of the classification, in agreement with Stephenson (1930, p. 719), seems unwarranted by our present knowledge.

Pickford and Avel, as well as Stephenson, inadvertently reveal in their discussions a more immediate need for distinguishing two groups of oligochaetes. Three sets of terms have been used in the past: Terricolae and Limicolae, Megadrili and Microdrili, higher and lower oligochaetes. Many species obviously of earthworm size (sometimes as much as 12-18 mm. thick) and of terricolous habit formerly were considered to be microdrile or limicole. By 1930 Stephenson admitted it was sometimes convenient to include moniligastrids in the Megadrili. Later Yamaguchi (1953, p. 331) added the Haplotaxidae, Alluroididae and Syngenodrilidae. The terms indicative of size no longer are inappropriate though a very few microdriles may be somewhat larger than smallest megadriles. The Haplotaxidae, Alluroididae and Syngenodrilidae as well as the Moniligastridae, for more than thirty years, have been lumped together by the writer (*cf.* Gates, 1959) as "earthworms". No common word for "non-earthworms," however, has been available. Yamaguchi's division of the oligochaetes, which is in agreement with the author's practice, provides an appropriate pair of terms. The Megadrili, accordingly, includes the fourteen families of earthworms that are now recognized (Gates, 1959). The Microdrili comprises the remaining oligochaete families including the Acanthobdellidae. The megadrile group is the exact equivalent of Yamaguchi's *Opisthopora diplotesticulata* and of Michaelsen's *Opisthopora*. The latter was defined circuitously and, like other suborders and series, on vast extrapolations from very little data.

Megadrili and Microdrili, in the author's usage, are only convenient terms to facilitate communication. Accordingly, they require no formal definition or morphological characterization.

Family MONILIGASTRIDAE

This megadrile group has been conspicuous among classical families because of its homogeneity. Isolation from other oligochaetes was recognized early and the family could have been better defined as long ago as 1895 from information then available. Nevertheless, unique structure enabling recognition of isolation

has not yet been mentioned in a formal definition. Diagnostic characters are: intraseptal location of testes and male funnels, delimitation of an ovarian chamber from peri-esophageal and neural coelomic spaces, presence of enterosegmental organs, median union of last pair (or each of last two pairs) of hearts above the gut to open into dorsal trunk indirectly through a short vertical vessel. All of those characters were retained by the most aberrant individuals that have been found. In contrast to so much uniqueness, other megadrile families are defined by no single diagnostic character or by just one for a group (Megascotlecidae) in which distinctive organs are lacking in parthenogenetic morphs.

A moniligastrid character, perhaps less likely to be unique, is provided by the prostomium. That organ, presumably as a result of considerable deepening and subsequent posterior extension of a slight transverse groove that once provided demarcation from the peristomium, is now attached to the roof of the buccal cavity behind level of intersegmental furrow 1/2. Still protrusible, and also capable of assuming a sucker-like shape, the moniligastrid prostomium at present appears not to be homologous with the longer and slenderer proboscis of certain glossoscolecids.

Absence of seminal vesicles is not confined to the Moniligastridae as those organs have disappeared in recent parthenogenetic morphs of several families. Extra-esophageal blood vessels are also lateral to the hearts in *Syngnodrillus* and may prove to be similarly located in other genera when long neglected vascular systems are studied. The single-layered clitellum, yolky ova, and location of male pores in front of the female apertures are all characters supposedly shared with the Alluroididae and Haplotaxidae as well as microdrile families.

Each portion of a moniligastrid septum containing a testis and male funnel has been called a testis sac. That characterization originally was given to, and in most megadriles still refers to, a truly coelomic space, containing one or both testes and male funnels of a segment, bounded by membranous or muscularized partitions, in communication with the exterior by an aperture in the funnel and the narrow gonoduct lumen as well as a minute male pore. Such a sac often is formed by development of partitions that seal off one (an unpaired sac) or two (paired sacs) ventral portions of the coelomic cavity. In various other megadriles the sac results from a series of gradual evolutionary changes such as approximation (or apparently so) of parietal

insertions of two consecutive septa, apposition of the septa peripherally finally followed occasionally by abortion of dorsal portions of the united septa. In all such cases the coelomic cavity of a particular segment is more or less markedly reduced but without affecting size of the metamere or diminishing total volume of coelomic space. Ocnero-drilid testis sacs are of a different sort. Each is merely a testis much enlarged by retention of developing gametes. The sac is a solid protuberance from the posterior face of the septum and may reach considerable size, even large enough to have been mistaken on various occasions for seminal vesicles. Any internal space (not artificially produced) that may appear is, of course, schizocoelic and not coelomic. The sac, unlike the seminal vesicles, is not in communication with the coelom nor does it open to the exterior. Sperm are released into the coelomic cavity by rupture of the sac wall and pass to the exterior via gonoducts that open to the interior and exterior as usual. The moniligastrid sac likewise is solid, any spaces not produced by preservation, fixation or dehydration, etc., in preparation for sectioning, again must be schizocoelic. Differences from the ocnero-drilid sac are two. First, the developing germ cells are proliferated, not posteriorly, but into the interior of a septum which becomes bulged anteriorly as well as posteriorly and more or less equally (if conditions permit) into two consecutive coelomic cavities. Second, the sac also contains a male funnel on which the testis sometimes even seems to be seated. Sperm no longer are released into the coelom to run the risk of ingestion by amoebocytes. Moniligastrid and ocnero-drilid testis sacs obviously are not homologous with any of the various kinds found in other megadriles.

The cavity of the moniligastrid ovarian chamber, unlike any schizocoelic spaces that may be present in otherwise solid testis sacs, is coelomic. The chamber, in more primitive forms, seems to be still bounded by the parietes peripherally but is closed off mesially from peri-esophageal and neural portions of the coelom that are omitted in figures purporting to show similarity to the testis sac. The chamber is closed off, in more advanced forms, from the parietes and then is arched like a horseshoe over the gut with one limb passing ventrally on each side. The ovarian segment is just as large as the one next behind, hence there is no reduction in size, merely a rearrangement of internal partitions. Complete closure of the chamber, rather curiously, does provide at maximal distension much more space for yolk and ova than had been available before.

Anatomy of the enterosegmental organs has been studied only in one species, *D. nepalensis* (cf. below). Function is unknown and the noncommittal name is intended only to indicate that they are metamerically repeated and are on the gut, into which each component may open at one or both ends.

The esophagus, in most megadriles studied by the author and also in South African acanthrodrilids (Pickford, 1937), ends in a narrow valve that must relax to allow passage of ingesta into the intestine. As moniligastrid gizzards long had been said to be at the beginning of the intestine, a valve was sought in front of the first gizzard but was not found. A narrowed portion of the gut much like a valve, concealed from view by deep sacculations of adjacent portions of the gut, eventually was located some distance behind the last gizzard. Thereafter, all of the gut between pharynx and the valve, regardless of length, was regarded as esophageal. The cuticular lining has been traced from the gizzards through several segments but not as yet all the way to the valve or to the buccal cavity. Determination of the segment of intestinal origin proved to be much more difficult than in other megadriles, partly because of close crowding of septa, partly because of delicacy of septa and of distended gut wall in material often not well preserved. Even in specimens carefully fixed in a relaxed condition, variation in location of the supposed valve was found. This perhaps should have been anticipated because of variation in gizzard location. The data secured from laboratory as well as field-preserved material were insufficient to show correlation between location of gizzard and valve. Situation of the supposed valve, in desmogasters and hastirogasters, as far back as the region xxv-xlii, suggested more careful examination of structure throughout the entire anterior portion of the gut. That, unfortunately, soon became impossible. However, if gizzards are at the beginning of the intestine, the esophagus has been extended in some lines of moniligastrid evolution from xii to xxv,² or through more segments than in bringing the gizzard of the supposed haplotaxid ancestor of the megadrili from v back into xii. There may then be no need for assuming disappearance of a more anterior gizzard and evolution of other, and perhaps intestinal, gizzards behind gonad segments.

Moniligastrid vasa deferentia, though often longer than in any other family, open at or close to the intersegmental furrow next behind the funnel septum. During their growth the male ducts

² An individual series of 2-12 moniligastrid gizzards may be anywhere in xii-xxx.

pass (always?) into the segment in front of the funnel septum. In certain circumstances the ducts conceivably could acquire external openings in that metamere so as to be in front of the testis septum. As an individual aberration (*Drawida* sp.) male pores sometimes are closer to the testis septum and so are in the position characterizing series *Lumbriculina* in Michaelsen's *Prosopora*. Situation of male pores does not now appear to be a proper character for defining suborders and their sections or series. One rather common and widely transported lumbricid even has the pores in front of the female apertures in agreement with the moniligastrids.

Moniligastrid prostates also are different from glands bearing that name in many megadriles. The structure appears to be more like that of the eudrilid euprostates except for presence on the coelomic face of a glandular tissue. Moniligastrid and eudrilid prostates usually have been said to be enlarged terminal portions of the male deferent apparatus which is correct only from the viewpoint of superficial appearance. Male gonoducts in the Oligochaeta (so far as is known) grow away from funnel rudiments and eventually to or through the parietes. Prostates, except in the Megascolecidae (where mesodermal origin is diagnostic), probably always are centripetal growths from the body wall. Proof of that origin, even in absence of information about developmental stages, is provided for the Eudrilidae as well as the Moniligastridae by occasional presence in adults of "prostates" that are not associated with male gonoducts.

Spermathecae of three moniligastrid genera, though monaxial, as in various microdrile and megadrile families, always are distinguished by location of the ampulla dorsally. Additionally, the duct always is longer than the distance between ampulla and spermathecal pore and often is much longer, a condition for which no explanation has been proffered. A secondary axis, when present (*Drawida* and *Moniligaster*), always lacks a special seminal chamber and so is different from the diverticulum of acanthodrilid, octochaetid and megascolecid spermathecae.

Most moniligastrid peculiarities were recognized in field-preserved material. As microscopic anatomy is studied in proper preservation, other typical characters are likely to be found, especially in the excretory system but perhaps also in the musculature. Formal expression of the uniqueness and isolation from other earthworms in more elaborate classifications would seem to require, as was recognized by Yamaguchi (1953), recognition of a taxon *Moniligastrina*.

Ovisacs, always dorsal, at maturity often extend back through several segments and are filled (in the many specimens that were examined by the author) not with ova but with granules of several sizes. These particles, long believed to be yolk, are of unknown chemical nature. After the breeding season the granules gradually disappear and the formerly distended sacs collapse. Massive production of yolk now appears to be another moniligastrid specialty.

The vascular system, in spite of some apparent generic differences with regard to the hearts, does conform strictly to a family pattern, as the last pair always is two segments in front of the ovarian metamere. Genital ducts, male and female, open to the exterior variously but always in conformity with the pattern. This means, in effect, that moniligastrid genera still are distinguishable, as in the past, only by location of the gonads. In contrast, the status of each genus similarly distinguished in other families now is suspect.

Rather large segment numbers now appear to be characteristic of the moniligastrids. The smallest desmogaster (86-115 by 4.5 mm.) has more than two hundred metameres, and the smallest drawida (30-41 by 1.5 mm.) has more than a hundred.

Habitats. Moniligastrids were believed (cf. Stephenson, 1930, p. 608) to need "moister conditions than any other family of earthworms, taken as a whole," presumably because of lack of dorsal pores — "usually connected with an aquatic habitat." The moisture requirement was deduced from casual site records and absence of species in the drier regions of India. Dorsal pores are indeed lacking in the limicoline Criodrilidae and Sparganophilidae but also are absent in the Hormogastridae as well as two large families, the Eudrilidae and Glossoscolecidae, that are mainly if not entirely terricolous. Almost any sort of earthworm is likely to be found at supposedly typical drawida sites, mud, under stones in water, in saturated soil by a spring, etc., during periods of drought. One introduced drawida now is established at Lahore where precipitation is less than twenty inches a year. In the dry zone of central Burma drawidas are common but the war prevented publication of data as to habitats. Burmese desmogasters certainly are not limicolous and probably most drawidas also are terricolous.

Distribution. India to Korea on the Asiatic mainland, Japan, Borneo, Sumatra. Absence of endemic species in the Philippines, Java and other Malaysian islands, even the Andamans, should

not be assumed until earthworms have been collected more systematically in those areas.

The range, with the exception of Sumatra, is the same as of the best known genus, *Drawida*. Ranges of other genera are much smaller and except for that of the South Indian *Moniligaster* apparently with internal discontinuities. However, few more than a hundred specimens (even if as many as that) of *Eupolygaster*, *Desmogaster* and *Hastirogaster* have been studied.

The distributions provide little support for the classical belief that *Drawida* is the youngest genus, or for its descent from *Moniligaster*.

Genus *DRAWIDA* Michaelsen 1900

Sites of the testes, in the smallest juveniles that have been examined, were indicated by opacities in septum 9/10 near to or about at the usual ventral position of oligochaete gonads, i.e., near parietes and mesially. The septal thickening is larger in longer juveniles and higher up in the body. At maturity, the sac now markedly protuberant from the septum, usually is just above the gut.

Although the male pore is only one segment behind the testis septum, the vas deferens always is much longer than the distance between gonad and aperture, occasionally a hundred times or more longer. The gonoduct, as it leaves the male funnel, often passes downward for a short distance in a schizocoelic intraseptal space but apparently always emerges into the coelomic cavity of the preseptal segment where it is farther away from the site of its future opening to the exterior. Within that anterior metamere continued growth seems, judging from adult conditions, to have been random, looping the duct back and forth, up and down, even around the heart. Eventually, the duct passes back through the gonad septum and always enters the prostate of its own side. Before attaining that junction in some species, the duct penetrates into the body wall where it may join the prostate or turn back into the coelomic cavity. As the duct always reaches its proper gland, regardless of presence of similar glands nearby, a later portion at least of its growth seems no longer to have been aimless but directed. Control presumably is provided by some sort of attraction emanating from the prostate. If that influence is exercised while prostatic anlage are confined to the parietes, junction may take place there, after which some prostates, by their own further growth, carry an ectal

portion of the gonoduct back into the coelomic cavity again. Junction with other prostates appears to be acquired only after gonoducts and glands had emerged independently into the coelom. In such cases, attraction presumably still emanated from growing ental portions of the anlage which had gotten into the coelom before gonoducts had acquired junction. Unexplained, however, is the apparently invariable passage of gonoducts from the funnel septum into the anterior segment where they are farther away from the level at which they will finally open to the exterior. Return of the gonoduct to the postseptal metamere, on the contrary, could be attributable to prostatic attraction. Whether the gonoduct reaches its greatest elongation in the coelomic cavity of *x* before or after junction with the prostate cannot now be stated.

The prostates, according to early accounts, have at least three layers, a middle muscular one, an inner glandular, and an outer glandular, the latter derived either from the inner layer or from the peritoneum. Origin of the inner glandular layer was not mentioned but doubtless is ectodermal. The middle layer of moniligastrid prostates, at least in early growth stages, may well be muscular but in adults of various drawidas is often thin, translucent or transparent, sometimes reddish and brittle. The color, as in the clitellum, may have been "developed" after preservation but the peculiar texture seems "unlikely to have resulted from a post-mortem modification of muscle tissue. Whether muscular or otherwise, the middle layer gives to the prostates a wide variety of shapes, one of which seems to be characteristic in each species. The outer glandular layer completely covers the coelomic face of the capsule in some species, but in others is more restricted to an ental portion or to some rather definite zone or area.

Digitiform prostates, present in some species of each genus except *Moniligaster*, have been thought to be primitive. GM glands of one drawida, identical in structure with the supposedly primitive prostates except for the blind ental ending, were thought to show descent of the bitesticulate *Drawida* from the quadritesticulate *Desmogaster*. The latter genus has testes in septa 10/11-11/12 but extra prostates in the supposedly derived *Drawida* were so placed that testes would have been in septa 8/9-9/10. More recently, prostate-like glands were found (in other species) in segments vii-ix as well as in *x* where, alongside the real prostates, they are supernumerary. An extra gland

in x, closed entally just like the glands in vii-ix, obviously cannot be "the thickened terminal part" of a male gonoduct. Such an appearance, however, can be achieved if gonoducts during their centrifugal growth penetrate into apices of developing capsular glands.

The "prostates" in some species of *Drawida* (and also of *Desmogaster*) have no glandular investment but whether these "muscular" glands(?) are capsules that have lost the outer glandular layer is unknown.

Spermathecae of some drawidas are monaxial but ducts are slightly widened within the parietes. A similar thickening presumably was the rudiment from which a secondary axis was developed in various lines. This still reaches, in an early stage of evolution, only a little above the body wall but now is joined on one side by the slender spermathecal duct. A more obvious secondary axis, as well as an ectal portion of the male terminalia in various microdriles, long has been called an atrium. Spermathecal atria are thin-walled organs that may be digitiform or saccular and much longer or thicker than the main axis, or even thick-walled chambers that sometimes become bifid. Each atrial bifurcation, in a species group not otherwise presently distinguishable from *Drawida*, bears a dichotomously branched outgrowth that presumably is glandular. The atrial aperture of other species, in a distinctly demarcated genital marking, has been withdrawn into a preatrial (!) parietal invagination. Sperm rarely have been found in the atria and then only in an ectal portion. Function of the spermathecal atria is unknown but is unlikely to be the same as that of spermathecal diverticula in other megadriles which have a more or less distinctly demarcated seminal chamber solely for storage of the sperm received in copulation.

Ovaries of all drawidas always are in segment xi (abnormality excluded). This character, uniquely diagnostic among earthworms, greatly puzzled classical oligochaetologists, and has further consideration in a subsequent section.

Distribution. The natural range, as already noted, is that of the family, with exclusion of Sumatra, and is much larger than that of the supposedly all conquering megascolecid *Pheretima*. Transportation, presumably by man, has resulted in the following additions to the natural range: Aru, Soemba, Caroline Islands, Bahamas, and Puerto Rico.

Taxonomic Characters

The latest key to species of *Drawida* (Stephenson, 1923, pp. 127-130) has 48 couplets or triplets for 42 of the 43 species then known. Even so, all data except that in the original description was disregarded in entering *D. ghatensis* Michaelsen 1910. Many other species, it is now clear, would have been equally refractory if specimens additional to very short series or the unique type had been dissected. Brevity of early descriptions (often still unsupplemented) and immaturity (usually unrecognized) of types, in which definitive genital structure was incompletely developed or even undifferentiated, added to the difficulties.

Several classical characters, such as shape and position of testis sacs, shape of prostates (except when muscular), latitudinal location of female pores, presence or absence of dorsal pores, now are known to have no taxonomic validity. Relative widths of intersetal intervals, as Stephenson admitted, may differ from one part of the body to another as well as from one worm to another and also may vary according to degree of contraction or relaxation at preservation. Other characters are of little use because of limitation to presence or absence, as in the case of pigment and peripheral closure of ovarian chamber, or because condition of material often does not allow a decision as to which of those pairs is involved. The taxonomic value of characters provided by gizzards (number, location) and genital markings (number, location, shape, size), even after accumulation of considerable data, still remains to be determined.

Shape of muscular prostates, latitudinal location of spermathecal and male pores, as well as atrial characters, do have some, more or less limited use. Spermathecal pores may be at *B*, *mBC* or *C* but in Burmese worms are, with one exception, at the lateral level. Male pores may be at *B* (one Burmese species) or between *B* and *mBC* where differences are too small and variable to be useful. Spermathecal atria may be subject to considerable intraspecific modification. Thus, a slight symmetrical thickening of an ectal portion of the spermathecal duct has become, in the northern part of the *caerulea* range, a muscular diverticulum that is larger than the original axis. Great intraspecific variation in length of digitiform atria has been found in two of the better known species. Thin-walled saccular atria, on the contrary, are of about the same shape and size in a number of species.

The characters allowed to have taxonomic value by classical authorities, as Stephenson's key proves, were too few to enable recognition of relationships. Other characters now appear to be of greater significance. Length of male gonoducts may be distinctive in some species but confirmation is required as great intraspecific variation has been found in two of the better known forms. Entrance of male gonoducts into parietes prior to junction with prostates, emergence into the coelom before joining, intraparietal junctions that are concealed or obvious, now appear to be specifically invariable, but ducts of all Burmese species enter prostates directly, i.e., in the coelom without first passing into body wall. Shape of capsule in glandular prostates seems to be free of intraspecific variation but in many Burmese species is digitiform. More ectal portions of the deferent apparatus can provide a number of characters. Male pores in an apparently primitive stage are superficial, minute and recognizable with difficulty due to absence of differentiated structure around them. Often, areas containing the pores are protrusible in more or less characteristic shapes. Such porophores in a retracted state, and especially when delimited by deep grooves, have a rather discoidal appearance. Differences between states of complete protrusion and retraction, when unrecognized as such, have been thought to distinguish species (cf. synonymy of *nepalensis*). Adequate characterization still is impossible for some Burmese forms, in spite of examination of numerous specimens, because one or the other of the states has not been seen. Primary male pores may be invaginate and then the larger superficial apertures provide another character. Existence of parietal invaginations is suspected in certain species. In others a short ectal portion of the prostatic duct may prove to be eversible as a sort of penis. Deeper invaginations that were ignored or undetected by earlier authors also furnish important characters; penial bodies, tubular penes, genital markings and even glands may be present in chambers that reach into the coelomic cavities. Determination of relationships between muscular prostates and the coelomic copulatory chambers, as for instance in *D. caerulea*, may provide further characters.

An ectal portion of the spermathecae may repay more careful examination than it usually has had in the past. The primary spermathecal pore of one Burmese species is invaginated and the shallow parietal chamber contains a distinctly delimited genital marking.

Glands associated with epidermal genital markings provide a set of characters in addition to absence. Tubular glands, once thought to be prostates, have obvious though minute pores that were thought to be male pores. Size, relative to that of the real prostates, may be specifically distinctive. Solid glands have no lumen and presumably no aperture. The wall may be transparent to translucent or opaque and then is soft or tough. Shape and size, especially of the tough-walled glands, may vary in a single specimen but the condition of the outer layer now appears to be uniform within a species. Clear glands (with transparent walls) apparently do not become as large as the others and may be buried so deeply in the parietes as to be unrecognizable from the coelom without removal of most or all of the longitudinal musculature.

The excretory system, as in other supposedly holonephridial families, has had very little attention. Early ontogenetic abortion of nephridia in segment ii may prove to be common if not universal in the family. Later disappearance of organs in one or more segments of the genital region now seems likely to provide a set of taxonomically useful characters. Nephridia are vesiculate and the bladder is a diverticulum (or caecum) given off from the tubule shortly before entering the parietes in the few moniligastrids for which information has been recorded. Caecal bladders may prove to be characteristic of the family. Parietal portions of nephridial ducts now seem more likely to be of interest to systematists. Ducts enter the body wall near the ventral setae of postgenital segments in several species of *Desmogaster* and *Hastirogaster*. Entry, in anterior segments of a Japanese drawida, now is near the lateral setae though still at the lower level in postgenital segments. In two Burmese drawidas, for which information still is available, the parietes is entered, in postgonadal segments, at the lateral level. Within the body wall ducts may or may not pass directly to an epidermal aperture. In the latter case ducts grow ventrally or dorsally for some distance before finally turning towards the epidermis. Irregular alternation of nephropores between two or even three levels, usually with more or less asymmetry, has been found in several species. Nephropore locations, accordingly, need not indicate levels at which ducts enter the body wall.

Number of segments in types usually has been recorded. One type, 47 by 1.75 mm., has 150 segments. Another, 55 by 2 mm., has 165. The only record of less than a hundred segments (98)

is of a unique specimen that may be a posterior amputee. One Indian species was said to have more than 500 segments and five others have more than 300 or 400. Information available as to segments of *nepalensis* (129-180), *gracilis* (140-340) and other species does not suggest hatching with a definitive number. Much tedious counting doubtless will be required to determine specific limitations.

Color characterizations of the past often are of little or no importance to the taxonomist today. An unpigmented lumbricid species, *Octolasion cyaneum* (Savigny, 1826), by its name provides one bit of supporting evidence. Another lumbricid example is furnished by *Eisensia rosea* (Savigny, 1826) which usually appears to be unpigmented though minute yellowish or brownish (epidermal?) flecks often are recognizable under the binocular in older individuals. Colors sometimes mentioned, or occasionally shown in plates, are attributable to cuticular iridescence, blood, even to ingesta within the intestine or (especially at posterior end of the body) to accumulations of coelomic corpuscles and debris. A green color, apparently characteristic of a few species, cannot be traced to discrete particles. A beautiful red color of the clitellum in many drawidas is "developed" after preservation by formalin and perhaps also by other substances. The fine granules responsible for that color are in the outermost portion of the epidermal cells. Similarly located granules may be responsible for a striking orange or red coloration of the clitellum in live specimens of *E. rosea* but after preservation the pigment flecks appear to be yellowish or brownish.

Pigment usually is in or is associated with the circular muscle layer of the body wall but may extend into the longitudinal layer at the anterior end and dorsally. Presence of granules that appear to be red or reddish brown in sections through the body wall does not always confer a similar color. Such worms often seem to be blue, sometimes even a quite dark blue or almost black. The clitellar region, at maturity, of pigmented drawidas after preservation may be white though pigment is present underneath the epidermis.

A clitellum rarely has been recognized *in vivo* and moniligastrids were for a time placed in a group called Aclitelliens. The tumescence that has sometimes been noted in preserved specimens may have been developed by the preservatives. Except as interrupted by genital markings, the clitellum probably

is always annular in the Moniligastridae. Though intergeneric differences have been recognized they do not now appear to be of taxonomic importance.

Certain characters not mentioned in the taxonomic section as they now appear to be universal throughout the family are: absence of typhlosoles, supra-intestinal and calciferous glands; location of extra-esophageal blood vessels lateral to the hearts; presence of a subneural trunk that is adherent to the parietes rather than to the nerve cord as in the Lumbricidae. Seminal vesicles, possibly present in some ancestral form before direction of proliferation by the testes was reversed, always are absent. Penial and copulatory setae never have been found.

DRAWIDA BEDDARDI (Rosa)

- 1890. *Moniligaster beddardii* Rosa, Ann. Mus. Sto. Nat. Genova, 29:379.
(Type locality, Chiala, Burma. No types.)
- 1894. *Moniligaster beddardi*, Bourne, Quart. Jour. Micros. Sci., 36:374.
- 1895. *Moniligaster barwelli* (part), Beddard, A Monograph of the Order of Oligochaeta, p. 200.
- 1900. *Drawida barwelli* (part), Michaelsen, Das Tierreich, 10:116.
- 1923. *Drawida barwelli* (part), Stephenson, (The Fauna of British India), Oligochaeta, p. 133.
- 1924. *Drawida barwelli* var. *hehoensis* + *D. "fluvaitilis"* Stephenson, Rec. Indian Mus., 26:324, 325. (Type localities, Heho plain and White Crow Stream, both near Yaungwhe. Types in the Indian Mus.)
- 1926. *Drawida teeta* Gates, *Idem*, 28:148. (Type locality, Yaungwhe. Paratype in U. S. Natl. Mus.)
- 1931. *Drawida hehoensis*, Gates, *Idem*, 33:340.
- 1933. *Drawida hehoensis*, Gates, *Idem*, 35:443.

The type locality of this species was said to be "Villaggio di Chiala 1400-1500 m (Carin Padaung o Ascuii Gheeu)." The district mentioned was not a political division and reference presumably was to some area inhabited by Padaungs seventy-odd years ago when Fea was collecting in Burma. It may have been almost anywhere between Leiktho Cirele and Karenni. The village probably passed out of existence long ago. No information about it was obtainable in Burma and a better guess than that above could not be made by Italian missionaries stationed at the area in question.

All drawidas found on the Shan Plateau during 1925-1940 were referred to three species, *hehoensis*, *longatria* and *nepalensis*. The latter two are clearly distinguished from *beddardi*

by length of their male deferent ducts and by the genital markings as well as associated glands. The color mentioned by Rosa provides no clue and may have been unnatural (preservation was alcoholic). The dorsal pores supposedly present doubtless were the "small dark spots" noted by Stephenson in his material. The "labbra rigonfie" of the type may well have been tumescences such as occasionally were recognizable in *hehoensis*, around the secondary male apertures. With these clarifications there remains no morphological or distributional contra-indication to suppression of *hehoensis* as a synonym of *beddardi*.

D. barwelli, with which *beddardi* was mistakenly synonymized, was never found in Burma.

Each male pore of the classical authors opens into an invagination comparable to copulatory chambers of various pheretimas. The much smaller primary pore is at the free end of a penis pendent from chamber roof. The penis is protrusible through the secondary aperture and the chamber itself is ever-sible. Male porophores at maximal protrusion, presumably as during copulation, have the penes projecting from a thicker basal portion. External apertures of the spermathecae, no longer minute, are large enough to admit a distal portion (at least) of the porophore into what appears to be a thickening of a parietal portion of the spermathecal duct. This chamber has been called an atrium but the structure bearing that name in many species of *Drawida*, although much larger, does not serve as a vagina.

DRAWIDA BULLATA Gates 1933

1933. *Drawida fucosa* Gates, Rec. Indian Mus., 35:439. (Type locality, Kalewa, Burma. No types.)

Prome, September, 2-26-4. K. John.

Laboo (Prome), September, 0-0-13. K. John.

Thanbula (Thayetmyo), September, 12-30-46. K. John.

Taungdwingyi (Magwe), August, 0-0-12. K. John.

Minbu, August, 13-27-10. K. John.

Ye-U (Shwebo), August, 13-27-10. Saw San Thwe.

External characteristics. Size (juveniles excluded), 65-95 by 4-5 mm. (Minbu), to 94 by 4 mm. (Taungdwingyi), 55-65 by 3-4 mm. (Ye-U), 84-120 by 4-5 mm. (Laboo), 90-180 by 4-7 mm. (Thanbula), 150-180 by 4-7 mm. (Prome). Unpigmented. Nephropores, present from iii, on anterior margins of segments, at or close to *D*. Clitellar coloration, red, extending into ix and xiv.

Spermathecal pores, very small transverse slits, just median to *C*. A marginal area, forming a circumferential lip, is clearly marked off peripherally and often is so protuberant that the pore appears to be located on a transversely elliptical, small papilla. This usually seems to be segmental as it is bounded posteriorly by 7/8 but may be situated exactly on 7/8 with no more indication of belonging to vii than to viii. Only an anterior portion of such a lip is marked off, on most Minbu worms, by a transverse groove, concave posteriorly, that does not pass into 7/8. These lips or protuberances may be only slight evolutions of the spermathecal ducts rather than definite porophores. Female pores, minute, circular, in transverse areas of greyish translucence, at or just lateral to *B*.

Male pores, transverse slits on ventral ends of whitened, anteroposteriorly flattened, rather pointed protuberances in *BC*, with median margins nearer to *B* than lateral margins are to *C* and often reaching *B*. Each porophore is bounded posteriorly by the presetal secondary furrow of xi and in front apparently (most specimens) by 10/11 which curves anteriorly around the porophore. On other worms 10/11 seemingly is continued just onto the median and lateral faces of the porophore where it becomes unrecognizable, the porophore bounded anteriorly by a groove that opens into 10/11 just beyond those blind endings. On such worms the male pore is in line with 10/11 and the porophore accordingly appears to be formed from parts of both x and xi though that from x is much the smaller. Porophores on other worms appear to belong wholly to xi, the male pores much nearer anterior than posterior margins. The porophore is delimited anteriorly, in Taungdwingyi worms, by a transverse furrow near posterior margin of x that does not pass into 10/11 but here also the larger part of the porophore obviously is from xi. Solid or other definite glands always are lacking in porophores of this species.

Genital markings, whitened areas of epidermal thickening, distinctly delimited as a rule but not associated with special glands, in (viii)-ix-xii (cf. Table 1). Markings of x usually are paired: transversely oval and with pointed end mesially, in median half of *BC* but sometimes reach *A* or into *AA*, in the postsetal annulus (Minbu, Taungdwingyi); longitudinal, reaching to or almost to *B* and *C* and through setal-postsetal annuli (Prome, Laboo, Thanbula, Ye-U) or confined to postsetal annulus (1, Ye-U). Paired markings of xi are transverse,

usually smaller than in x, in a median part of *BC* but occasionally reaching *A*, confined to setal or to setal-postsetal annuli. Unpaired and median markings are transverse, usually extending through setal-postsetal annuli (in which case the presetal annulus is quite short), reaching well into *BC* or even to *C*. A pair of markings that do not quite meet at mV, in viii of one Laboo worm and in ix of one Minbu worm, if united would be of the same size as the unpaired markings. On the right side of a Thanbula worm the marking of x is small and transverse but the marking of xi is large and longitudinal, the reverse of the usual condition as well as of that on the left side.

Internal anatomy. Gizzards, 1-3, in xv-xviii (Table 2). Three gizzards of a Prome specimen that may prove to belong to this species are in xviii-xx.

Testis sacs, usually unconstricted, about equally in ix and x. Vas deferens, slender, usually iridescent in 9/10 and in ix, in a number of short loops on anterior face of 9/10 median or close to or around hearts of ix. Occasionally, further loops (Minbu) are bound by connective tissue in a small cluster against posterior face of 9/10. A more ectal, non-iridescent and seemingly thickened portion in x, less than 5 mm. long, is slightly sinuous, zigzagged or in several short loops and passes into ental end of prostate directly. The cluster of hair-pin loops of the thickened portion in x of worms from other localities may be about half the size of the testis sac above it (Ye-U, Prome), smaller to nearly as large (Thanbula), as large to larger (Laboo, Taungdwingyi). The thickened portion in a Ye-U worm is 60+ mm. long. Prostates, protuberant into coelomic cavity and usually bent over towards the nerve cord, narrowed only within the parietes, ental end bluntly rounded, shortly elliptical in cross section, occasionally with an appearance of slight anteroposterior flattening, glandular investment continued to body wall. Capsule, usually reddish, soft, digitiform, slightly curved, 1 (Taungdwingyi, Minbu) to 2 mm. (Prome, Thanbula) long.

Spermathecal atria, digitiform, in vii. Atria are erect on anterior face of 7/8, irregularly constricted or very shortly zigzag-looped and less than 5 mm. long (Minbu), or are in a clump of shortly u-shaped loops bound to ventral parietes. The cluster may be small and ventral or large enough to reach to or almost to dorsal parietes. Length, 10-20 mm. (Ye-U), 10-12 (Prome), 15-20 (Taungdwingyi), 60-70 mm. (Laboo). A terminal portion about 10 mm. long in some Laboo worms is filled with

a sticky white material in which slight spermatozoal iridescence is visible.

Ovarian chamber, closed off from parietes. Ovisacs, extend into xiv or xv.

Juveniles. Greyish translucent spots, anlage of male pores, are at 10/11 in the two smallest juveniles on which no porophores or protuberances are recognizable. Male porophores of larger juveniles are represented by slight swellings of anterior margin of xi without definite posterior demarcation, the pores now apparently behind 10/11 which seems to be bent forward slightly around the protuberances. If segment x contributes any part to the male porophore it certainly must be much smaller than that from xi.

Juveniles still without genital markings have male gonoducts of about the same length as those of acitellate and clitellate worms from the same locality.

Remarks. The smallest adults are from a southern portion of the species range where there is considerable rainfall. The largest were found in regions of much less precipitation.

Some acitellate worms (3 Taungdwingyi, 2 Ye-U, several Thanbula) appear otherwise to be fully mature.

From the postseptal portion of male gonoducts, in worms softened after long formalin preservation, a sheath had separated off so as to reveal internally a slightly zigzagged or sinuous tube of about the same thickness as the preseptal portion.

Male porophores have been seen only in a protuberant state, presumably just as at copulation. Information as to the completely retracted state is needed.

D. fucosa was distinguished from *bullata* by quantitative differences such as soma size, length of spermathecal atria and of male gonoducts. Individuals as small (20-45 by 1½-2 mm.) as most of those on which *bullata* was erected are unlikely to copulate with worms as large as the types of *fucosa* (130-170 by 6-7 mm.) but intermediate soma sizes herein reported make retention of *fucosa* unnecessary. Variation in lengths of spermathecal atria and vasa deferentia parallels that recorded below for *longatria* from which *bullata* is distinguished by absence of solid GM glands. Relationships to *vulgaris* remain uncertain.

Abnormality. (No. 1.) Left spermatheca, with two ampullae (distended by white material), one attached to posterior face of 7/8 in usual manner, other hanging down in coelomic cavity, each with a discrete duct 1½ mm. long, the united duct passing ventrally as usual.

TABLE 1

Frequency distribution of segmental position of median and paired genital markings in *D. bullata*

	Median		Segments		Paired	
	ix	x	xi	xii	x	xi
Prome (30)					30	30
Laboo (13)	7		3	1	13	10
Thanbula (76)	11		4	19	76	72
Taungdwingyi (12)	12				12	12
Minbu (37)	25			8	37	37
Ye-U (9)	3	2		3	7	9

Figures in parentheses, number of specimens from the locality.

TABLE 2

Frequency distribution of segmental position and number of gizzards in *D. bullata*

TABLE 2

Locality	xv	Segments			Number of gizzards		
		xvi	xvii	xviii	1	2	3
Taungdwingyi	5	12			7	5	
Ye-U	9	11	2			11	
Minbu	14	27	28	2		13	5
Laboo	2	11	12	3		8	4
Thanbula	2	15	18	7		15	4
Prome	5	17	18	12		5	14

DRAWIDA CAERULEA Gates 1926

Kayan (Hanthawaddy), August, 0-5-8. K. John.

Thongwa (Hanthawaddy), August, 0-6-8. K. John.

Thinbawgyin (Bassein), October, 0-0-6. K. John.

Pegu, August, 0-0-2. "Jungles to the east," 0-3-1. K. John.

Thanatpin (Pegu), August, 0-2-3. K. John.

Toungoo, October, 0-2-0. K. John.

Minbu, August, 0-0-2. K. John.

Myingyan, September, 0-0-2. K. John.

Myotha (Sagaing), September, 0-1-1. K. John.

Ava (Sagaing), September, 0-3-6. K. John.

Mandalay, September, 0-7-0. K. John.

Ye-U (Shwebo), September, 0-9-34. Saw San Thwe.

External characteristics. Nephropores, present from iii. Left male porophore of one Kayan worm is completely retracted though the right is completely everted. Genital markings, always lacking.

Internal anatomy. Pigment, always present in the body wall. Gizzards, one or two only in Ye-U specimens, with one exception and then three in xiv-xvi. Commissures from extra-esophageals, behind 8/9 (60 specimens).

Vas deferens, slender, iridescent, twisted into a small cluster of loops that are firmly bound together (southern localities), slightly thicker throughout but still iridescent and loops much less firmly bound together (Ava), slightly thickened and iridescent throughout but longer and loops easily separated, length 65-70 mm. (Ye-U).

The spermathecal duct of southern worms obviously is more thickened in a terminal portion than in species of the *beddardi* group. The thickened part is pyriform or almost conical and mainly in the body wall. In Ye-U worms the thickened portion is asymmetrical and reaches forward halfway to 6/7 and presumably must be called an atrium. Size of the atrium is less than half that of *rasilis* in which 6/7 and dorsal parietes are reached.

Ovisacs may extend as far back as into region of xix-xxii.

Abnormality. (No. 2.) Left male porophore, at 9/10. Left male organs, one segment anterior to usual location. Ovarian chamber, in two discrete halves, on the left side one segment anterior to usual location as is the female pore. An ovisac extends posteriorly from each ovarian chamber. Left spermatheca, lacking.

The left mesoblastic somite at the eighth level presumably was aborted during early embryonic development and its place was taken by the one at the ninth level.

Regeneration. Tail regenerate, of eight segments at 136/137.

Remarks. Data as to number and location of gizzards in specimens listed above were lost, as well as records that would have permitted characterization of prostates more adequately than in the past.

Male porophores of all previous southern specimens were fully protruded. Maximal protrusion and complete retraction now has been shown by a single worm (Kayan). The thick-walled muscular chamber into which the terminal half of the protruded porophore is withdrawn has been considered to be a prostate. This chamber is distinguished from the prostates of most moniligastrids by absence of a glandular layer on its coelomic face. Pending acquisition of further information about both kinds, the term prostate with characterization of "muscular" is retained.

Whether a porophore as large as that of southern worms can be inserted, without change of form, into the spermathecal atrium seems doubtful. The ejaculatory apparatus certainly appears to be highly evolved even though a discrete penis (such as is present in *beddardi*) is lacking. The atrium in *rasilis* is much larger than is required for reception of the porophore of southern worms but the protruded condition has not been seen in northern worms. Atria of *decourcyi* Stephenson, 1914, are even larger but here again only the retracted state of the male porophores has been seen.

Atrium now seems a more appropriate characterization for the parietal invagination into which the spermatheca opens through an aperture on a discoidal genital marking. The primary spermathecal pore may prove to be within the atrium and if so the external aperture will be tertiary rather than secondary.

Southern worms were distinguished from *rasilis* mainly by quantitative differences such as length of vasa deferentia and size of spermathecal atria. The range of *D. caerulea caerulea* as now known is from the Irrawaddy delta to latitude of Mandalay. *D. caerulea rasilis* was found in the Chindwin valley near Monywa. Worms from the region of Mandalay to Ye-U and Monywa are intermediate with respect to one or another of the characters distinguishing the two subspecies. Considerable searching through difficult territory much farther north may be required to reveal whether intermediate forms exist between *caerulea* and *decourcyi*.

DRAWIDA DELICATA nom. nov.

1930. *Drawida* sp., Gates, Rec. Indian Mus., 32, 298.

Remarks. A filament at distal end of each male porophore may be only cuticular lining of the spermidueal passageway that had been loosened and then evaginated during strong contraction at preservation. Whether such contractions protruded discoidal porophores normally extending into x-xi or everted small parietal invaginations is unknown. A "blueish shade" may not have been associated with pigment any more than in the unpigmented lumbricid, *Octolasion cyaneum* (Savigny, 1826). The "minute" size of spermathecal ampullae and shortness of ovisacs (in xii) may or may not be indicative of immaturity.

The species is distinguished from *beddardi* by the greater length of male deferent ducts, by absence of parietal invaginations at ectal ends of male deferent apparatus or, if male porophores are everted chambers, by absence therein of protrusible tubular penes. Elongation of the male gonoducts also distinguishes *delicata* from all other Burmese species with adiverticulate spermathecae except *spissata*. The latter requires no consideration because of great differences in spermathecae and prostates. Relationships presumably are with species yet to be collected in the little known areas west and south of Mergui district.

DRAWIDA FLEXA Gates 1929

Zinba (Tavoy), September, 0-0-1. W. D. Sutton.

Siyigyan (Tavoy), "plains" September, 0-1-3. W. D. Sutton.

Kawletchaung (Tavoy), "nearby hills," September, 0-4-5. W. D. Sutton.

Pyinthadaw (Tavoy), "nearby hills," September, 0-2-1. W. D. Sutton.

Nyaungdon (Tavoy), September, 0-0-1. W. D. Sutton.

Migyaunglaung (Tavoy), "plains," September, 0-1-0. W. D. Sutton.

Thaton, September, 0-0-2. K. John.

Duyinzeik (Thaton), September, 0-14-7. K. John.

Naunggala (Thaton), September, 0-3-3. K. John.

Bilin (Thaton), September, 0-15-12. K. John.

Taungzung (Thaton), September, 0-8-15. K. John.

Kinmunsakhan (Thaton), September, 0-0-7. K. John.

Boyagyi (Thaton), September, 0-1-0. K. John.

Kyaikto (Thaton), September, 0-12-4. "Nearby hills," September, 0-8-15. K. John.

Sittang (Thaton), October, 0-2-0. K. John.

External characteristics. Size may be rather small, as in worms from Kyaikto hills, 50-80 by 3-4 mm. (diameter measured across clitellum which is much wider than the rest of the worm). Nephropores, present from iii, in anterior margins of segments, usually at or close to *D*, pores of viii always dorsal to *D*, pores of ix usually at or only slightly dorsal to *D* but occasionally one or both dorsal and, more rarely, even farther from *D* than in viii. Dark spots at m*D* and near some preclitellar intersegmental furrows may look more or less like dorsal pores but epidermis and cuticle are imperforate even when there seems to be a gap in the musculature. Clitellar coloration, lacking ventrally on x and a presetal portion or all of xi, from a level just beyond lateral margin of male pore lips. Laterally from that level the epidermis is quite tumescent.

Spermathecal and male pores, larger than nephropores, certainly larger than female pores and accordingly not minute, margins of pores almost never smooth. Spermathecal pores, just median to *C*, at 7/8 or (apparently) just in front of 7/8. Male pores, at 10/11, close to *mBC*, longitudinally or transversely slit-like or irregular, each at center of an indistinctly delimited but nearly circular, white and slightly tumescent area reaching to or nearly to *B*, to a tertiary furrow on postsetal secondary annulus of *x* and the presetal secondary furrow of *xi*. The porophore is usually divided into two portions by 10/11 but when tumescent the furrow may be indistinct or even unrecognizable, especially close to the pores. The portion in front of 10/11 is lacking in Sittang worms.

Genital markings, usually transverse, 2 to 20, located as follows: Median (unpaired and rarely longitudinal), presetal in *viii* and *x-xii*, postsetal in *vii-x*, occasionally in setal annuli of *vii* and *x*. Paired, in *BC*, presetal in *viii-xii*, postsetal in *vii* and *x*, in setal annuli of *viii-xi*, in median half of *BC* (postsetal markings of *vii*, presetal of *x-xi*, those in setal annulus of *x*), or with centers nearer *mBC*. Duyinzeik and Taungzun worms have 16-20 markings each.

Internal anatomy. Gizzards, three (4 specimens), four (55), five (10), in *xvi-xxiii* (Table 4). Commissures from extraesophageals, in front of 8/9.

Vas deferens, short, slender, and for most part iridescent (clitellate specimens), in several loose loops on anterior face of 9/10, twisted around heart of *ix*, several further loops on posterior face of 9/10, an ectalmost portion 1-2 mm. long apparently slightly thickened and certainly without recognizable iridescence. Prostates, erect, recumbent or held against parietes by delicate strands, J- or U-shaped, entalmost portion of capsule only slightly or not at all widened.

Spermathecal atria, small, usually 1-2 mm. long, in Taungzun worms occasionally reaching a length of 3 mm. An ental portion, about half the length or slightly less, usually distended and with thin wall. Lumen gradually narrowed and wall thickened in ectalmost portion. Spermathecal duct, passing into posterior face of atrium in *vii* close to parietes.

Reproduction. Ampullary coagulum of clitellate worms usually is characterized by a rather brilliant iridescence presumably spermatozoal. Spots of iridescence also are clearly visible in the coagulum within distended ental portions of the spermathecal atria in several Taungzun worms. Iridescence of male gonoducts

TABLE 3
Location of genital markings in *Drawida flexa*

Locality	Paired											Unpaired				
	Presetal			Setal			Postsetal		Presetal			Setal		Postsetal		
	viii	ix	x	viii	ix	x	vii	x	viii	x	xi	xii	x	vii	viii	ix
Taungzun	15	18	13	8	10	11	11	1	15	6	13	1	9	11	1	18
Bilin	—	3	16	16	11	6	13	—	—	4	3	13	—	—	—	13
Duyinzeik	—	4	8	5	7	—	2	—	1	7	11	—	—	1	—	1
Kimunsakhan	—	1	7	2	5	2	2	—	—	—	—	—	—	—	—	—
Kyaikto	—	4	3	6	6	2	1	1	5	7	5	—	—	2	—	—
Naunggala	—	—	1	2	2	2	—	1	—	—	2	2	2	1	—	—
Hills 1½ miles from Kyaikto	—	4	—	17	13	7	1	1	—	12	14	4	—	8	13	—
Sittang	—	1	1	1	—	—	—	—	1	2	—	1	—	—	1	—
Kyaikto	—	5	2	—	—	1	—	5	—	1	2	—	6	—	2	1
Kyaikto town	—	5	6	12	3	3	—	2	1	2	6	8	1	—	—	1
Thaton	—	—	2	2	2	—	1	—	1	—	—	—	—	1	—	—
Tavoy No. 1	1	3	2	—	1	3	—	3	—	4	2	—	—	—	—	2
“ No. 2	5	5	3	3	1	1	—	6	—	7	7	—	1	—	—	3
“ No. 3	2	2	2	1	2	3	—	3	—	3	3	—	1	—	—	—
“ No. 4	2	4	2	1	1	—	—	3	—	5	3	—	1	—	—	—

Localities of numbered batches from Tavoy district cannot now be stated. The key, as well as the specimens, were destroyed during the war in Burma.

presumably is due to presence of sperm on the way out from the testis sacs. As sperm are matured and exchanged in copulation, reproduction is assumed to be sexual and biparental.

Regeneration. The only record now available is of a tail regenerate, at 170/171, with terminal anus and 36+ segments.

The difference in thickness of ectal and ental portions of spermathecal atria, and of the shape, is so little that the organ can be called digitiform. A similar slight distention of an ental portion sometimes was recognizable in much longer atria of *bullata* and *longatria*.

The *flexa* range in Burma appears to be restricted to the Tenasserim division and there from Tavoy north to the Sittang River. The Thailand boundary may not be a natural boundary for the species.

Relationships are with *longatria* from which *flexa* is distinguished by the smaller genital markings, smaller size of the glands associated with those markings, absence of a gland in male porophores and shortness of spermathecal atria. Atria are of about the same length in several races of *longatria* but not in those found in the *flexa* range. Additional differences may be recognizable when retracted states of *longatria* male porophores can be seen. Although differences are quantitative, all specimens from the Tenasserim division have been referable, without question, to one or the other of the species involved.

TABLE 4

Frequency distribution of segmental position and number of gizzards in *D. flexa*

Locality	Segments								Number of gizzards		
	xvi	xvii	xviii	xix	xx	xxi	xxii	xxiii	3	4	5
Duyinzeik (17)	1	6	12	17	17	15	3		2	10	5
Taungzun (22)		6	17	21	22	18	6		1	18	3
Pyinthadaw (3)		2	3	3	3	1				3	
Naunggala (6)		1	5	5	6	6	2		1	3	2
Kawletchaung (9)		4	8	8	9	5	1	1		9	
Siyigyan (4)		1	4	4	4	3				4	
Miscellaneous* (8)		2	7	8	8	6	1			8	
Totals	1	22	56	66	69	54	13	1	4	55	10

* Includes: xvii-xx (1 Migyaunglaung, 1 Thaton),
xviii-xxi (2 Sittang, 1 Thaton, 1 Boyagyi, 1 Zinba),
xix-xxii (1 Nyaungdon).

DRAWIDA GRACILIS Gates 1925

Thaton, September, 23-0-0. K. John.

Kyaikto (Thaton), September, 1-0-0. K. John.

Thongwa (Hanthawaddy), August, 24-4-0. K. John.

Twante (Hanthawaddy), September, 1-0-0. K. John.

Hlawga (Insein), September, 4-0-0. K. John.

Wanetchaung (Insein), September, 5-0-0. K. John.

Taukkyan (Insein), September, 7-1-0. K. John.

Thinbawgyin (Bassein), October, 0-3-0. K. John.

Pegu, August, 38-0-0. "Jungle to the east," 60-0-0. "Jungle to the west," 33-0-0. K. John.

Thanatpin (Pegu), August, 9-0-0. K. John.

Paukkaung (Prome), September, 9-0-0. K. John.

Prome, September, 11-0-1. K. John.

Thanbula (Thayetmyo), September, 5-3-0. K. John.

Sadoway, "Hills," September, 19-0-0. I. M. Ismailjee.

Ramree (Kyaukpyn), "nearby hills," September, 1-0-0. I. M. Ismailjee.

External characteristics. Nephropores, present from iii. Clitellar coloration, red, lacking ventrally on x and presetal half of xi. Male porophores of the clitellate specimen are protuberant, rather conical but with rounded distal ends, firm but containing no glands. Porophores of less mature worms are more nearly discoidal but possibly because adult organization had not been completely achieved.

Genital markings, indistinctly delimited areas of epidermal thickening, paired, transverse, between *B* and a level just beyond lateral margin of male porophores, in the presetal annulus of x, anterior portion of the postsetal annulus of x, setal annulus of xi but extending forward into presetal annulus and occasionally almost to the intersegmental furrow. Markings in x of the clitellate specimen meet mesially, a slight furrow along mV the only indication of a boundary. The ventral setae are included in the anterior markings. The epidermis in a presetal portion of ix (Prome, clitellate) or viii and ix (Thongwa, a clitellates) is thickened in *BB* or even *CC* but no markings are recognizable externally. A longitudinal marking, in a median portion of *BC* (3 Pegu specimens), extends through the whole length of x as on one of the types.

Internal anatomy. Gizzards, two (1 specimen), three (26), four (6), in xiv-xx (Table 6). Intestinal origin, in xxi (specimen with gizzards in xiv-xvii), just behind 21/22 (specimens with gizzards in xiv-xvii and xiv-xvi). Commissures from extraesophageals, in front of 8/9.

Vas deferens, slender, rather long, twisted into two clusters of closely compacted loops, one on each face of 9/10, clusters of about the same size or the anterior slightly larger, the two together smaller than the testis sac, slender throughout. Prostates, sessile on parietes, of circular outline, capsule small, 0.5-1.25 mm. long, shortly ovoidal, pointed end within the parietes.

Spermathecal atria, digitiform, 1.0-1.5 mm. long, lumen narrow, an irregular cleft in transverse section. Ovisacs (clitellate worm) reaching into xvii.

Abnormality. (No. 2.) Male porophores, two pairs, on 10/11 and 11/12, each porophore with a minute, transversely placed male pore. Greyish translucent spots in 11/12 at *B* just median to margins of male porophores are about at sites of female pores. Testis sacs of 9/10 are normal but in the region where 10/11 should be there is on each side of the body a fairly large cluster of loops of a second vas deferens that is not connected at all with the anterior male gonoduct. The prostate, on each side, is a single acinous mass extending slightly across levels of inter-segmental furrows 10/11 and 11/12. The anterior vas of a side passes into the anterior margin, the second into the posterior margin of the prostate. Paired ovisacs extend into xiv.

Ovaries and oviducal funnels were not distinguishable, in part perhaps because of poor preservation. Relationships of septum 10/11 to 11/12, to the gut, and to the parietes were not determined.

Gonads of xi may have been hermaphroditic.

Remarks. Length of fully mature worms is unknown, since only anterior portions of aclitellate and clitellate individuals were obtained. Absence of mature specimens in collections from

TABLE 5

Frequency distribution of segmental position of genital markings in *D. gracilis*

Locality	x		Segments	xi
	presetal	postsetal		
Thongwa	3	8		8
Taukkyan		6		6
Prome	7	7		7
Thanbula	2	2		2
Hlawga	2	2		2
Pegu	1	4		4
Paukkaung	3	3		3
Thinbawgyin		3		3

so many localities may have been due to failure to dig deep enough.

Some geographical variation in a range as large as that of *gracilis* would not be unexpected.

TABLE 6

Frequency distribution of segmental position and number of gizzards in *D. gracilis*

Locality	Segments							Number of gizzards		
	xiv	xv	xvi	xvii	xviii	xix	xx	2	3	4
Thanbula (3)	3	3	3						3	
Thongwa (7)	3	7	7	4				1	5	1
Pegu (15)	2	6	11	14	10	5	2		10	5
Prome (5)		4	5	5	1				5	
Taukkyan (1)			1	1	1				1	
Thinbawgyin (2)			1	2	2	1			2	
Totals	8	20	28	26	14	6	2	1	26	6

DRAWIDA LONGATRIA Gates 1925

External characteristics. Nephropores, obvious, present from iii, except on x of adults, at or very close to *CD* except in viii where they are somewhat more dorsal. A longitudinal dark band of rather blueish appearance (as if pigment were showing through the epidermis) usually is visible at mD except in the most anterior segments. Also visible at mD, close to various anterior intersegmental furrows, are markings that look more or less like dorsal pores.

Internal anatomy. A discrete longitudinal muscle band at mD is lacking. Instead, the longitudinal muscle layer gradually becomes thinner toward mD and just at that level is almost *non-existent*. This thinning is responsible for the externally recognizable dark band at mD. Close to intersegmental levels at mD, especially anteriorly, after stripping off the longitudinal musculature, there are visible slight protuberances or depressions but cuticle and epidermis are not perforated, i.e., dorsal pores are lacking.

The gut behind the pharynx is rather slender, in viii-x with low but lamelliform longitudinal ridges on inner wall. The gut is valvular, in individuals of the nominate race having gizzards in xv-xviii, through all of xxii or of xxiii.

The dorsal trunk is single anteriorly until disappearance into tissues of the pharyngeal bulb. The subneural, usually large

and blood-filled, is adherent to the parietes. Even before removal of the cord, the trunk usually is recognizable in contracted specimens as closed ends of the loops protrude beyond each side of the cord. Nephridia, apparently vesiculate behind the elitellum, bladders perhaps elongately sausage-shaped (condition poor and relationships of parts not determinable with certainty). Nephridial duets, behind the elitellum at least, pass into parietes at *CD* gap. Nephridia were not found in x of adults and presumably are aborted prior to maturity. Brain and commissures to subpharyngeal ganglion were left posteriorly in iii by a transverse section exactly along 3/4.

Glands associated with genital markings have no lumen but are provided with a thick, tough and obviously muscular wall.

Remarks. As male porophores always have been more or less markedly protuberant the retracted states cannot yet be characterized. Because of appearances in specimens with less protuberance it is suspected that the primary male pores may be invaginated slightly in a state of complete retraction.

Supposed pores of GM glands, previously recorded, are now believed to have been artifacts. These "glands," without any lumen and thus called solid, may have mechanical rather than secretory functions, such as stiffening penes (certain Chinese species) or male porophores (*longatria*), gripping penes or porophores during copulation when present in walls of spermathecal pore invaginations (some Chinese species) or in the parietes close to the spermathecal pores (*longatria*).

Internal anatomy of all specimens available since 1941 is like that of the nominate race as characterized above.

Variation in shape, size and direction of male porophores, in size, shape and location of genital markings, is so great that attempts to define a few externally identifiable varieties were abandoned long ago. Many large collections from the recent alluvium in the deltas region south of Henzada-Tharrawaddy, secured after 1932, contained only individuals that were like the Rangoon types on which the species was erected. This material enabled recognition of a location pattern for genital markings though many individuals lack one or more of the set. An area somewhat larger than that just indicated had been delimited, before Pearl Harbor, as the probable range of a nominate race. Presence of the same form in places as far apart as Rangoon, Burma and Palembang, Sumatra, must be attributed to overseas transportation, presumably by man. The original source

obviously is Burma. Since habits are such as to permit transportation, and colonizing ability had been demonstrated, it was then possible to assume that presence of the nominate race in isolated Burmese localities such as Myitkyina, Bhamo, etc., likewise is a result of transportation. Disregarding such colonies which appeared to be localized in and immediately around towns to which potted plants are known to have been taken from Rangoon, delimitation of ranges of other races, usually found in less urban situations, was under way when the Japanese invasion ended local study of Burmese earthworms.

The races differ from one another in various characters, some of which are determinable only from dissection. Some of the differences have been thought to distinguish species. Male porophores probably are not exactly the same in any two races of which there are an unusual number.

DRAWIDA LONGATRIA LONGATRIA Gates 1931

External characteristics. Segments, 183 and 206, the last few metameres of each worm very small, without externally recognizable setae but showing no evidence of regeneration.

Spermathecal pores, not minute, transversely slit-like.

Genital markings: unpaired, median, presetal, in *AA*, of xi (6 specimens), xii (16), xiii (7); paired, each in median half of *BC* in xii (3), united marginally with a median marking (2), or rudimentary (1). An area of greyish translucence, in lateral half of *BD* or even reaching beyond *D*, in presetal annulus of viii lacks the distinctly demarcated rim of the other markings but is associated with a characteristic parietal gland. A less obvious area of epidermal modification, associated with a small gland, is present in the posterior part of vii just median to each spermathecal pore.

Regeneration. Three of the sixteen worms from Bhamo and Myitkyina, with 124, 171 and 172 segments, are unregenerate posterior amputees. Another individual had lost its hind end at time of collection. Ten of the twelve remaining specimens have tail regenerates. Number of segments in the regenerates: at 104/105, 86 setigerous + several very short and without externally recognizable setae; at 124/125, 23 + 7 or more; at 136/137, 14 + 6 or more; at 143/144, 16 + 6 or more; at 165/166, 6 + ?. The anus in each of those cases is terminal. Young regenerates at 142/143, 145/146, 151/152 and 152/153 each have a dorsoterminal anus that may reach nearly to the substrate.

Segments, usually without externally recognizable setae, usually are distinguishable only on the ventral side. The distance from substrate to dorsal margin of the anus, in a regenerate with indications of 10 + segments, is only about a quarter of the distance from substrate to ventral margin. One regenerate, at 196/197, is unsegmented.

Remarks. The two unamputated worms, with 183 and 206 segments, obviously had become sexually mature before metameric differentiation had been completed in a terminal portion of the body.

External characteristics. Length of worms from Tharrawaddy district, to 170 mm. Diameter, to 7 mm. Segments, 149 + a number of rudimentary metameres without externally recognizable setae, 177 + 1 or 2, 190 + several (3 specimens), 191 + 2 or more, 193 + 1 or 2, 206 + 2 or 3, 210 + 2, 211 + 2 (2 specimens), 220 + several.

Genital markings: unpaired, median, presetal, in *AA* of *xii* (2 specimens); paired, each in median half of *BC* or reaching to *A*, presetal, in *xii* (32), in *viii* where margin is indistinct as in Bhamo-Myitkyina worms (41), occasionally replaced by two or even three smaller markings, postsetal, in lateral part of *BC* in *vii* (41) and there small, even more indistinct than in *viii*.

Regeneration. Three worms are unregenerate posterior amputees. Thirteen worms had lost their hind ends at or since time of collection. Six of the remaining twenty-five have tail regenerates as follows: still unsegmented, anus reaching forward in dorsum nearly to substrate; anus dorsoterminal, segmentation indicated ventrally but setae unrecognizable externally; at 134/135, 10 setigerous segments + a number on which setae are unrecognizable, anus dorsoterminal; at 143/144, 12 + several; at 191/192, 3 + several; at 197/198, 5 + several.

Remarks. Each of the 19 unamputated worms has, immediately in front of the anal segment, one or more circumferential furrows that presumably are intersegmental. In the axial portions thus delimited, nephropores and setae are unrecognizable. The portion of the body in front of the anus then is a growth region in which metameric differentiation had not been completed when the worm became sexually mature.

These Tharrawaddy worms probably were secured in the plains.

DRAWIDA LONGATRIA VERRUCOSA Gates 1931

External characteristics. Segments, 205, 206, 213, 224, 225, 233, 237, 238, in each case with two or more rudimentary segments already demarcated but without externally recognizable setae.

Spermathecal pores, like the male apertures, small transverse slits. Male pores, facing anteriorly or anterolaterally. Tumescer margin of the male pore with a slight but definite groove coming out of the pore and passing posteriorly on ventral face of the tumescence. Male porophores, in *AD*, reaching equators of x-xi or shortened at either end. Each disc-like porophore may have an anterior and a posterior genital marking, or markings may scarcely be distinguishable though glands are present, or either marking and the gland may be absent.

Genital markings, additional to those of the male porophores, are as follows. Unpaired, median, in *AA*, presetal in viii (3 specimens), in setal annulus of viii (3), postsetal in x (11), xi (13), xii (17). Paired, presetal in *AA* of x (2, in *AB* of viii (3), x (13), xi (2), postsetal in x (15); larger and in some part of *AD* on each side, postsetal in vii (17), postsetal in viii (15, in two of which each marking is replaced by two smaller ones), presetal in x (4), presetal in xii (14).

Regeneration. One worm is an unregenerate posterior amputee and another had lost part of its tail at time of collection. Four have tail regenerates. One has no externally recognizable segmentation. Another, also with a dorsoterminal anus has several rudimentary segments (without setae) marked off ventrally. Two regenerates, at 198/199, have each a terminal anus; segments, 6 (+?) and 19 (+?).

Remarks. Each of the eleven unamputated worms has several rudimentary segments at its posterior end.

This series of seventeen specimens from Tharrawaddy district probably was secured in the hills or in jungles remote from the town.

DRAWIDA NANA Gates 1933

The GM glands have a soft, opaque wall without muscular sheen and may represent an intermediate stage in evolution from the "clear" sort with transparent wall to the *longatria* sort with a strongly muscularized wall. If, however, definite pores are present in the associated genital markings, as was originally believed, the glands will not be solid and will provide additional evidence for distinction from *longatria*.

DRAWIDA NEPALENSIS Michaelsen

1907. *Drawida nepalensis* Michaelsen, Mitt. Naturhist. Mus. Hamburg, 24:146. (Type locality, Gowchar, near Katmandu, Nepal. Type in the Indian Mus.)
1909. *Drawida nepalensis* + *D. burchardi* Michaelsen, Mem. Indian Mus., 1:147, 149.
1916. *Drawida jalpaigurensis* Stephenson, Rec. Indian Mus., 12:307. (Type locality, Jalpaiguri, at base of the eastern Himalayas. Type in the Indian Museum.)
1917. *Drawida nepalensis*, Stephenson, Rec. Indian Mus., 13:372.
1922. *Drawida nepalensis*, Stephenson, *Idem*, 24:430.
1923. *Drawida nepalensis* + *D. burchardi* + *D. jalpaigurensis*, Stephenson, (The Fauna of British India), Oligochaeta, p. 146, 134, 141.
1924. *Drawida troglodytes* Stephenson, Rec. Indian Mus., 26:129. (Type locality, Siju Cave, Garo Hills, Assam. Type, in the Indian Mus.)
1925. *Drawida burchardi* + *D. hodgarti* + *D. papillifer* (part), Stephenson, *Idem*, 27:50, 51.
1926. *Drawida cacharensis* Stephenson, *Idem*, 28:251. (Type locality, Katlicherra, South Cachar, Assam. Types, in the Indian Mus.)
1929. *Drawida nepalensis*, Stephenson, *Idem*, 31:229.
1930. *Drawida nepalensis*, Gates, *Idem*, 32:290.
1931. *Drawida nepalensis*, Gates, *Idem*, 33:348.
1933. *Drawida burchardi*, Gates, *Idem*, 35:426.
1934. *Drawida nepalensis* + *D. troglodytes*, Gates, *Idem*, 36:242 and 253.

Andaman Islands

Port Blair, Station B 10, 2 specimens. Station B 15, 0-1-0. (Indian Mus.)
 Station 6, 1-0-0. (Indian Mus.)
 (No station indicated), September 1932-May 1933, 0-1-0. H. S. Rao. No data, 0-1-0. (Indian Mus.)

Burma

Sandoway, riverside, September, 0-1-0. Hills, September, 0-6-1. I. M. Ismailjee.

Akyab, September, 0-16-17. I. M. Ismailjee.

Myohaung (Akyab), September, 0-0-7. I. M. Ismailjee.

Naba (Katha), nearby hills, September, 0-2-0. Saw San Thwe.

Lashio (Northern Shan States), 7th mile on the Namtu road, September, 0-3-15. Wan Hu Mone village, 5 miles from Lashio, muddy ground covered with water cress, September, 0-0-1. H. Young.

E Nai village (North Hsenwi State), 9 miles from Lashio, at base of bamboo clumps, September, 0-5-20. H. Young.

Bhamo, September, 0-4-8. K. John.

Myitkyina, September, 0-0-14. K. John.

Weshi (Myitkyina), October, 0-3-0. F. D. Forbes.

India

Lokra (Balipara Frontier Tract, Assam), 8.xi.1939, 0-2-0. S. L. Hora (Indian Mus.)

Teesta Bridge, Teesta Valley, 2/6/34, -49-1. S. L. Hora (Indian Mus.)

Nagrota (Kulu District, Punjab), garden of P. W. D. rest house, 13/6/26, 0-1-0. S. L. Hora (Indian Mus.)

Pakistan

Lahore and vicinity, 29-16-13. H. K. Bhatti.

External characteristics. Size (Pakistan), 78-105 by 4-5 mm. Segments (Pakistan), 86 (posterior amputee), 113 (p. a.), 114 (p. a.), 129, 130, 137, 138, 139, 140, 144, 153, all juvenile, 135, 145, 148, 150, 154, 156, 157, 158, 159, 161, 162, 163, 164 (2 specimens), 166 (2), 168, 169, 173, 176, acitellate and clitellate specimens. Setae (Pakistan), closely paired, $AB = CD$, $AA > BC$, DD ca. = $\frac{1}{2}C$, unrecognizable in last three or four segments. Nephropores, present from iii, at *D* except slightly more dorsal on vii (Pakistan) or vii-viii (Burma), usually lacking (or unrecognizable?) in x (Burma) or x and xii (Pakistan) though quite obvious in xi. A pore definitely is present on right side of xii (1, Pakistan) and vestiges of pores of x sometimes become visible after treatment with picric acid.

Male porophores of most specimens are as previously described by the author and in a condition that must now be regarded as of maximal or near maximal protrusion, presumably as during copulation. Porophores of one Pakistan worm, almost if not fully retracted, are circular to shortly elliptical areas distinctly delimited from x and xi, depressed slightly below general epidermal level. Segments x and xi are slightly indented so that short anterior and posterior portions of the porophore are concealed from view. More indentation, if further change is possible, presumably would result in complete coverage of porophores which might then appear to be in some sort of a chamber.

Genital markings are of at least two sorts. 1) Small, circular areas of greyish translucence, one in each male porophore and one in vii just in front of each spermathecal pore. Around each of the anterior markings there often is a fairly wide and opaque band of slight epidermal thickening. The translucent area is the outer face of a nearly spheroidal solid "gland" filled with greyish translucent tissue. Porophore markings occasionally are not recognizable though the glands are present. Anterior glands may bulge the body wall up into the coelom or may be visible internally through gaps in the musculature. Glands of vii were

not found in several Arakan specimens but epidermis at sites of markings is slightly tumescent and wrinkled. 2) Areas of slight epidermal modification and not associated with solid or other glands. Two small transverse markings (Burmese worms) in each setal annulus of x and xi, about in line with the male porophores, epidermis slightly thinned. A median, transversely elliptical marking (many Pakistan worms) reaching *A* or *B* on each side in presetal half of xi, epidermis slightly thickened and without clitellar coloration. Paired, translucent areas of epidermal thickening in lateral part of *BC* or reaching *D*, presetal in vii (Lashio).

Five Arakan worms have a median presetal marking of variable shape and size in *AA* of ix. A central portion of each is translucent. Removal of the longitudinal musculature disclosed in the remaining thin portion of the body wall only a translucent spot which may be a vestige or rudiment of a gland.

Internal anatomy. A special longitudinal muscle band is lacking at mD where there is a gap in the musculature from 3/4 or 4/5 posteriorly that is of about the same appearance as those at setal levels. The gap is slightly widened just behind intersegmental levels. Removal of the longitudinal musculature discloses a slight protuberance at mD just behind level of each intersegmental furrow. The protuberance is over site of a somewhat pore-like marking which is behind rather than at intersegmental level. The cuticle and epidermis are imperforate, hence there are no dorsal pores.

A low rather broad median ridge is present on the floor of the esophagus in middle segments of the region behind the last gizzard. Gizzards, two to four (Table 7), in types of *cacharensis* are located as follows: xiv, xvi, xviii (2 specimens); xiv-xv, xviii (1); xiv, xvii-xviii (1); xiv, xviii-xix (1); xv, xviii (1); xvii, xix (1). Intestinal origin (Lokra worms), in xxiv (1 specimen), xxv (1), xxvi (3), xxvii (5). Enterosegmental organs in four or five postgizzard segments are especially obvious.

Dorsal blood vessel, probably complete but traceable only into iv. Ventral trunk, complete, bifurcating over subpharyngeal ganglion, the branches traceable along the circumpharyngeal nervous commissures nearly to the brain. Subneural trunk, adherent to parietes, traceable anteriorly only into x or ix. Commissures from extra-esophageals, in front of 8/9. From each posterior commissure a vessel may pass back on dorsolateral aspect of gut into xii or xiii, with four transverse connections

to the corresponding vessel of the opposite side. One of those paired vessels usually is unrecognizable, perhaps because it is empty rather than absent. The vessel that is visible is near the median plane and presumably is the one believed in the past to be a supra-esophageal. Hearts, of vi-ix lateral. Nephridia, lacking in x, vesiculate, bladder (usually called a caecum) elongately sausage-shaped. Nephridial ducts, pass into parietes at *D*.

One testis sac occasionally is displaced posteriorly underneath the ovarian chamber (13 Akyab specimens, neither sac displaced in 22 Akyab worms). Vas deferens, slender and iridescent in 9/10 and ix, with several small loops on anterior face of 9/10, one loop encircling heart of ix, thickened in x and there opaque, twisted into a cluster of loops that may be as large as the testis sac. Prostatic capsule, slenderly club-shaped, only very slightly and gradually widened entally, 2-4 mm. long.

Spermathecal atria, 3-5 mm. long, reaching into contact above gut or overlapping slightly, an ectal portion of variable length stalk-like, the widened ental portion usually irregularly constricted. Spermathecal ampullae (Pakistan), empty, translucent. Ovisacs (Pakistan), apparently reaching back into xiv-xv but actually within pockets of 12/13. Contents of distended ovisacs consist of yolk granules of several sizes. Ova, if at all present, certainly must be very few (acitellate as well as elitellate worms). Female funnels, vertically elongated and band-like, on posterior wall of the chamber from parietes to opening into ovisac, lateral margins folded over toward each other so as to form a sort of trough almost closed. Ovaries (preservation poor) apparently band-like and placed vertically opposite the female funnels. No egg strings were found.

Juveniles. Male porophores, on most of the Teesta juveniles, are represented by very small swellings on which the pores but not the genital markings are visible. Each swelling is demarcated anteriorly as well as posteriorly by a slight transverse furrow that does not pass at either end into 10/11. The latter is continued, on each side of the porophore, nearly to the tip and the male pore. Deepening of intrasegmental grooves and extension to 10/11 along with obliteration of 10/11 in the porophore presumably would produce the appearance characteristic of adults, of belonging neither to x nor xi. The male pores now are assumed to belong morphologically at 10/11, with the porophores originating about equally from x and xi.

Testis sacs, in the smallest Pakistan juveniles, just below the gut, gonoduct loops about at site where the testis would be in

other families. Ovisacs in juveniles of some size still are unrecognizable and the ovarian chamber apparently is not closed off peripherally. Oviducal funnels are recognizable but ovaries were not found.

Abnormality. Five helicometameres are present in the intestinal region of a Pakistan worm.

Regeneration. Head regenerate of six segments at 6/7 (Myitkyina). Tail regenerate, 5 mm. long (Arakan).

Parasites. Crescent-shaped, uninucleate protozoans are present (Arakan worms) in numbers on the dorsal face of the gut near the dorsal blood vessel.

Remarks. Variation in segment number is similar to that of *longatria*.

Septa from 10/11 posteriorly though membranous are strong enough to allow considerable anteroposterior movement of a postgenital portion of the gut—in one Pakistan worm the gut of xii-xiv and including a gizzard is in front of the ovarian chamber. Preservation, in the case just cited, was such as to permit tracing septa to insertions on gut as well as parietes thus enabling recognition of morphological location of the gizzard. Septa in the postgenital region often are adherent to the gut beyond the real insertions which may not always have been identified correctly. Even if all discontinuities in the gizzard series are mistaken the condition responsible for the erroneous determinations is characteristic of many individuals of *nepalensis*.

Male porophores of adult worms previously identified as *nepalensis* by the author were markedly protuberant presumably as during copulation. One of the Pakistan worms now has shown the retracted condition of the porophores.

D. cacharensis is known only from the type series comprising 16 (3 previously dissected) a clitellate (?) specimens. Differences from *nepalensis* are restricted to the male porophores. When protuberant, the porophores are like those of the author's *nepalensis* or slightly more conical. The genital marking sometimes is unrecognizable but the solid gland is present. Retracted porophores are as in one of the Pakistan worms. Similar porophores of the unique type of *troglydites* then are also in a retracted state. There now is no contra-indication to synonymization of *cacharensis* and *troglydites*. *D. jalpaigurensis* has been known hitherto only from the original account of a single a clitellate specimen "in a bad state of preservation." Examination of the type some years ago provided the data recorded below.

Addendum

External characteristics. Spermathecal pores, transverse slits at 7/8, slightly median to *C*. Male pores, not recognizable. Male porophores, transverse, very slightly raised, reaching mesially near to *B* and laterally at least to *mBC*, 10/11 continued slightly into the median margins but not into the lateral margins. Anteriorly and posteriorly each porophore is bounded by a definite, crescentic furrow concave towards the porophore, neither furrow passing into 10/11 mesially or laterally. A distinctly demarcated circular area just behind level of 10/11 in each porophore is the outer face of a tough-walled ovoidal gland protuberant into coelomic cavity, narrower and buried in the parietes. Genital markings, paired, presetal in vii, postsetal in vii and there just in front of each spermathecal pore.

Internal anatomy. Vas deferens, short. Glandular investment of the prostate, much thicker than the slender capsule. Spermathecal duct, in vii passing into posterior face near parietes of a saccular erect atrium. The gland of the postsetal genital marking of vii (labelled atrium in Stephenson 1923, fig. 51, p. 141) protrudes slightly into the coelom.

Remarks. Except for apparent shortness of the male gonoducts no evidence was found to justify retention of *jalpaigurensis*.

Forma ABSCISA Gates 1931

Kutkai (Northern Shan States), Dak bungalow grounds, ca. 4500 feet, November, 1926, 0-0-1. H. S. Rao (Indian Mus.).

Namkham (Northern Shan States), streams and pools on the north bank of the Shweli River, ca. 2500 feet, December 1926, 0-0-8. H. S. Rao (Indian Mus.).

Lashio (Northern Shan States), 0-3-0. H. Young.

Myitkyina and vicinity, September, 0-4-2. K. John.

Kadranyang (73rd mile on road from Myitkyina to Putao), October, 0-3-0. F. D. Forbes.

Kawa pang (82nd mile on same road), October, 0-5-0. F. D. Forbes.

Nawngkhkai (250th mile on same road), October, 0-15-0. F. D. Forbes.

Hting bai (92nd mile on same road), October, 0-7-0. F. D. Forbes.

External characteristics. Nephropores, present from iii. Spermathecal pores, transverse slits with smooth margins (acelitellate specimens) exactly on 7/8. Male pores, very small transverse slits but quite obvious and in concave depressions of ventral faces of protuberant porophores.

Genital markings here also are of two sorts: 1) Associated with a solid gland as in *nepalensis*. Very small, circular, greyish translucent areas in vii-viii close to 7/8 and near the spermathecal pores. One marking always is present in the vicinity of each spermathecal pore but there may be one or two more. 2) Circular, opaque and indistinctly delimited markings, unpaired even though not median, with a small translucent central spot and not associated with glands. These markings are lacking on ten of the worms.

Internal anatomy. Gizzards, three to five in xiii-xix (Table 9). Commissures from extra-esophageals, in front of 8/9.

Reproduction. Spermathecal ampulla of previous specimens, even though elitellate, were in a juvenile condition. No sperm were found in the spermathecal atria or spermathecal ducts and no externally adhesive spermatophores (as in all other species of *Drawida*) ever were seen. Parthenogenesis was suspected but in *Drawida* recognition of male sterility is not as easy as in some other genera. Testis sac coagulum was examined for evidence of sperm but the data no longer are available.

Spermathecal ampullae of six acelitellate worms from Hting bai, Kadranyang and Kawa pang, are large enough to be considered of adult size. Each adult ampulla, except in one worm, is filled with a sticky white material which may have (2 specimens) a slight iridescence that presumably is due to presence of sperm. However, spermathecal atria appear to be juvenile, ovarian chambers are empty, and ovisacs are juvenile.

Remarks. Male porophores of all worms referred to *abscisa* were protuberant, presumably as in copulation. Though easily distinguishable from those of *nepalensis* in the protruded condition, little difference in shape or appearance is expected in completely retracted states. Differences of *abscisa* from *nepalensis* are mostly quantitative such as smaller size, fewer segments (?), absence of a solid gland in the male porophores. The seeming discontinuity of the gizzard series that characterizes a majority of specimens of *nepalensis* has not been found in individuals with *abscisa* male porophores. Both forms have been transported by man and the original home of each is unknown. The Myitkyina records do seem to suggest that the northern part of the district is near if not within the original range. However, other earthworms collected by Mr. Forbes between Myitkyina and Putao are all of peregrine species and all were secured in vicinity of government rest houses to which exotic plants in pots or tins are known to have been taken. Worms with *abscisa* characters have not been found outside of Burma.

The locality list might well have been much longer except for an unfortunate rivalry. The collections from a northern part of the Myitkyina district were made by a missionary after the end of the rains when earthworm activity (cf. Gates. 1960b) is mostly restricted to still moist sites. Certain reptiles being collected for a museum, at the same time and in the same area, had to be fed on earthworms. The missionary was getting too large a share of the limited supply wherever he went. A complaint lodged with the government that the missionary was a communist spy resulted in an order that he return at once to Rangoon.

TABLE 7

Location of gizzards and of intestinal origin in
Drawida nepalensis

				Segments					Locality
xiii	xiv	xv	xvi	xvii	xviii	xix	xx		
1	1			1					Pakistan
1		1		1					Lokra
	1	1		1				xxvi	Akyab
	3	3		3					Pakistan
	1	1			1			xxvi	Akyab
	1	1				1	1		Pakistan
	2		2		2				Pakistan
	1		1			1			Pakistan
		1	1	1				xxvi	Akyab
		1	1	1				xxvii	Akyab
		1	1	1				xxviii	Akyab
		1	1	1					Lokra
		1	1		1			xxvi	Akyab
		1	1		1			xxvii	Akyab
		1	1			1	1	xxvi	Akyab
		1		1					Pakistan
		1			1	1			Pakistan
			1	1	1			xxvi	Akyab
			1	1			1	xxvi	Akyab
			1	1			1	xxvii	Akyab
			1		1		1	xxvi	Akyab
			1		1		1	xxvii	Akyab
				1	1	1		xxvii	Akyab
				1	1		1		Akyab
				1		1			Pakistan
				3		3	3	xxvii	Akyab
Specimens	2	10	16	15	20	11	9	10	

TABLE 8

Location of genital markings in *D. nepalensis* f. *abscisa*

Segment	Intrasegmental position	Localities				
		N	T	Kd	Kw	L
vi	Postsetal, centered at <i>B</i>				1	
vii	Setal annulus, in <i>BC</i>				1	
	Postsetal, lateral half of <i>AA</i>		1			
	Postsetal, in <i>BC</i>			1	2	
viii	Presetal, in <i>BC</i>			1		
	Setal annulus, lateral half of <i>AA</i>		1			
	Postsetal, lateral half of <i>AA</i>				1	
	Postsetal, centered at <i>B</i>			1		
	Postsetal, in <i>BC</i>				3	
ix	Presetal, centered at <i>B</i>	2				
	Presetal, in <i>BC</i>	4				2
	Presetal, lateral half of <i>AA</i>		1			
	Presetal, median	1				
	Setal annulus, lateral half of <i>AA</i>		1			
	Postsetal, lateral half of <i>AA</i>		2			
x	Presetal, lateral half of <i>AA</i>		1			
	Setal annulus, lateral half of <i>AA</i>		1			
	Postsetal, median	1	1			
xi	Presetal, centered at <i>B</i>		1	1		
	Presetal, in <i>BC</i>		1			
	Setal annulus, in <i>BC</i>		2			

Localities: N = Nawngkhkai, T = Hting bai, Kd = Kadranyang, Kw = Kawa pang, L = Lashio.

Existence of usual two secondary furrows is assumed even if furrows are unrecognizable.

TABLE 9

Frequency distribution of segmental position and number of gizzards in *D. nepalensis* f. *abscisa*

Locality	Segments							Number of gizzards		
	xiii	xiv	xv	xvi	xvii	xviii	xix	3	4	5
Lashio (2)	2	2	2	2	2					2
Tingpai (7)	1	2	7	7	6	5	2	1	3	3
Kadranyang (2)	1	2	2	2	2	1			2	
Nawangkai (14)		12	14	14	14	7			9	5
Kawapang (5)		1	5	5	5	2		2	3	
Totals	4	19	30	30	30	15	2	3	17	10

DRAWIDA PAPILLIFER Stephenson 1917

DRAWIDA PAPILLIFER PAPILLIFER

Ramree (Kyaukpyu), nearby hills, September, 0-5-0. I. M. Ismailjee.

Akyab, September, 0-5-0. I. M. Ismailjee.

Kyauktaw (Akyab), September, 51 juvenile and acitellate specimens. I. M. Ismailjee.

Buthidaung-Maungdaw (Akyab), September, 0-4-0. I. M. Ismailjee.

Paletwa (Arakan Hill Tract), September, 29 juvenile and acitellate specimens. I. M. Ismailjee.

External characteristics. Nephropores, present from iii and in x, slightly dorsal to *D* in iii-vii and somewhat more so in viii, occasionally also in ix.

Spermathecal pores, transverse slits, exactly on or rarely just anterior to 7/8, slightly median to *C*. Male pores, longitudinal or diagonal, in x though but slightly in front of 10/11, at or just lateral to *B*, each usually in a semicircular, indistinctly delimited, whitened area with base at 10/11; occasionally a short transverse furrow just in front of the male pore provides an anterior boundary. Female pores, at *B*, just behind 11/12. in very slight transversely slit-like crevices.

Genital markings, small areas of greyish translucence, circular or shortly elliptical (and then transverse), with very slightly raised and narrow, opaque rims. Markings are located as follows: One, on posterior margin of x immediately lateral to the male pore (5 specimens from Akyab, 16 from Kyauktaw, 9 from Paletwa). As before, but just in front a second marking (20 Kyauktaw, 10 Paletwa). A third marking on posterior margin of x and just lateral to the last of the other two (1, Paletwa). One marking just anterior to male pore (11, Paletwa). One marking in setal annulus of x just lateral to *B* (3 Kyauktaw, 1 Paletwa). One marking on anterior margin of xi, on each side, centered in *AB* or at *B* (5 Akyab). A presetal median marking on xii (1 Paletwa). Other markings are transversely elliptical. One on vii just in front of each spermathecal pore (5 Akyab, 48 Kyauktaw, 22 Paletwa). One in viii just behind each spermathecal pore (4 Akyab, 46 Kyauktaw, 13 Paletwa). One in *AB* of vii, just behind equator on each side (5 Akyab). Presetal, on each side of vii in median part of *BC* (20 Kyauktaw) or centered at *mBC* (11 Kyauktaw), or in lateral half of *BC* (12 Kyauktaw). One in median half of *BC* in setal annulus of vii on each side (4 Kyauktaw). One postsetal on each side of vii in median half of *BC* (5 Paletwa) or in lateral half of *BC* (1

Paletwa) or even dorsal to *D* (13 Paletwa). One in setal annulus of vii, on each side, dorsal to *D* (2 Paletwa).

Internal anatomy. Pigment, present in circular musculature of dorsum even when a bluish color is unrecognizable or almost so externally.

Low longitudinal or vertical ridges are present on inner wall of a postgizzard portion of the esophagus. Gizzards and intestinal origin, respectively, are located as follows: xiii-xv and xxii (1 specimen), xiv-xvi and xxiii (10), xiv-xvii and xxiii (2) or just behind 23/24 (7), xv-xvi and just behind 23/24 or in xxiv (2), xv-xvii and xxiv (3), xv-xviii and xxiv (2), xvi-xvii and xxiv (3). Commissures from extra-esophageals, anterior to 8/9. From one of the posterior commissures (behind 9/10) a vessel usually passes back into xii or xiii along the dorsolateral aspect of the gut. This vessel often is close to the median plane and when distended with blood probably has been mistaken in the past for a supra-esophageal trunk. A corresponding vessel on the opposite side, in the present worms, may have been empty and hence unrecognizable. Nephridia are present in x.

One testis sac is displaced posteriorly into xii or even farther back in 59 specimens (juvenile, sexual and postsexual). Both sacs are displaced in 1 sexual specimen. Neither is displaced in 9 juveniles, 13 sexual and postsexual specimens. Vas deferens, short, probably about five and certainly no more than ten mm. long. The ental portion runs ventrally within or bound to 9/10, passes in front of heart of ix and then back into x where its short loops are in a small cluster against posterior face of 9/10 well above parietes. Prostates, erect, close to 9/10 so that the vas does not drop to or even very near the parietes though entering the gland below its ental end. Prostates, club-shaped, narrowed ectally, 2-3 mm. long (coelomic portion), capsule rather slender ectally, an entalmost portion of varying length slightly widened and almost spheroidal, shortly ovoidal, or rarely almost ellipsoidal.

Spermathecal atria, in vii, 2-3 mm. long. An ectal portion of variable length, rather slender and duct-like, may be fairly sharply marked off from the widened ental portion. The latter which may be of about the same length as, shorter or longer than the duct is slightly flattened and shortly or elongately elliptical to oval in outline. Whitish, sticky material within the ental portion of an atrium can be disentangled into a long cord. A slight iridescence (spermatozoal?) characterizes cords of one

worm. The coagulum in the spermathecal ampulla is not cord-like and though soft is teased apart only with some effort. Spermathecal duct, slightly widened just prior to passing through 7/8, length and thickness of widened portion slightly variable. Segment xi always open in pinned out worms (82) and the ovarian chamber appears not to be closed off peripherally.

Abnormality. (No. 2) Male pore and associated genital markings of left side lacking. Left spermathecal pore, at 8/9. Left testis sac, vas deferens and prostate, lacking (Paletwa).

Remarks. Distinguished from *peguana* mainly by the male pore locations.

Ramree worms and three from Kyauktaw are slightly different from other west Burma specimens and are briefly characterized below.

External characteristics. Spermathecal pores, apparently just behind 7/8. Male pores, nearer mBC than B. Female pores, slightly lateral to B.

A transversely elliptical (to almost circular) genital marking just median to each male pore, centered at or slightly lateral to B and reaching A, is larger than other markings of x in these and all other specimens. Small translucent spots, just anterior and posterior or posterolateral to each male pore may be rudimentary markings. Transversely elliptical markings located as follows: one just in front of each spermathecal pore (3 Kyauktaw, 4 Ramree); two in front of each spermathecal pore in a longitudinal series (2 Kyauktaw); one just behind each spermathecal pore (4 Ramree).

Internal anatomy. Gizzards in xv-xvii (3 Kyauktaw). Intestinal origin in xxiii (3).

Testis sacs, not displaced. Vas deferens probably shorter than in other worms as the cluster of loops on the posterior face of 9/10 definitely is smaller. Prostatic duct (portion of capsule without glandular investment), slightly longer.

Coagulum in spermathecal atria, with a slight iridescence, apparently not in a long coiled cord. Atrial stalk, much shorter than the ental sac.

GM gland median to male, enlarged and interrupting longitudinal musculature.

DRAWIDA PAPILLIFER PEGUANA Gates 1925

Migyaunglaung (Tavoy), plains, September, 0-5-0. W. D. Sutton.
Pynthadaw (Tavoy), hills, September, 0-0-1. W. D. Sutton.

- Kawlet chaung (Tavoy), nearby hills, September, 0-1-1. W. D. Sutton.
 Siyigyan (Tavoy), September, 0-0-6. W. D. Sutton.
 Kyaikmaraw (Amberst), August, 0-0-1. K. John.
 Thaton, September, 0-26-8. K. John.
 Duyinzeik (Thaton), September, 0-14-8. K. John.
 Naunggala (Thaton), September, 0-38-15. K. John.
 Bilin (Thaton), September, 0-5-6. K. John.
 Aungsein (Thaton), September, 0-6-2. K. John.
 Sittang (Thaton), October, 0-3-0. K. John.
 Boyagyi (Thaton), September, 0-7-0. K. John.
 Kyaikto (Thaton), September, 0-12-5. K. John. Nearby hills, 0-9 8. K. John.
 Kyaiktiyo (Thaton), September, 0-2-0. K. John.
 Taungzun (Thaton), September, 0-45-30. K. John.
 Kinmunsakhan (Thaton), September, 0-3-7. K. John.
 Kyauktan (Hanthawaddy), August, 0-16-0. K. John.
 Syriam (Hanthawaddy), August, 0-2-0. K. John.
 Twante (Hanthawaddy), September, 0-10-0. K. John.
 Kungyangone (Hanthawaddy), September, 0-7-0. K. John.
 Thongwa (Hanthawaddy), August, 3-0-0. Saw San Thwe.
 Dedaye (Pyapon), September, 0-1-0. Maung Ohn Maung.
 Maubin, October, 0-1-0. Maung Ohn Maung.
 Danubyu (Maubin), October, 0-0-1. Maung Ohn Maung.
 Wanetchaung (Insein), September, 0-6-0. K. John.
 Taikkyi (Insein), September, 0-4-0. K. John.
 Dam site (Insein), September, 0-5-1. K. John.
 Pegu, August, 0-6-1. K. John.
 Henzada, October, 0-1-0. Maung Ohn Maung.
 Ingabu (Henzada), October, 0-1-1. Maung Ohn Maung.
 Prome, September, 0-4-0. K. John.
 Labu (Prome), September, 0-28-6. K. John.
 Paukaung (Prome), September, 0-23-2. K. John.
 Pegu Yomas, from 10 miles south of Pyu, September, 0-0-5. G. E. Blackwell.
 Pegu Yomas, from 15 miles south of Pyu (Pegu), September, 0-10-3. G. E. Blackwell.
 Pegu Yomas, from 32 miles south of Toungoo (Toungoo), September, 0-0-1. G. E. Blackwell.
 Pegu Yomas, from 24 miles south of Toungoo (Toungoo), September, 0-2-2. G. E. Blackwell.
 Pegu Yomas, from 8 miles south of Toungoo (Toungoo), September, 0-1-0. G. E. Blackwell.
 Toungoo, October, 0-5-0. K. John.
 Kyaukkyi (Toungoo), October, 0-1-0. Saw Marshall Thwin.
 Sah Der, Karen Hills (Toungoo), September, 0-1-0. H. I. Marshall.
 Thayetmyo, September, 0-29-7. K. John.
 Thanbula (Thayetmyo), September, 0-12-2. K. John.
 Magwe, August, 0-10-16. K. John.

External characteristics. Size, of smallest, complete and clitellate specimen, 50 by 3 mm. Nephropores, present from iii, one or both of viii usually dorsal, rarely so in ix and then nearer *D* than in viii, apparently always present in x. An equatorial circle of tiny white spots is present in each segment from iii posteriorly.

Spermathecal and male pores, larger than female apertures and nephropores, have, in contrast to many other species of *Drawida*, smooth margins and a definite shape.

A whitened area just in front of and just behind each spermathecal and male pore (in x and xi from or just lateral to *B* to or just beyond *mBC*) is present on every specimen and has a definite boundary though not as a rule marked off by a furrow. The epidermis of those areas certainly is not thickened and may be slightly thinned. Genital markings always are present in the whitened areas. Additional markings may be present elsewhere (Table 10).

Internal anatomy. Pigment, in the circular muscle layer, lacking underneath white areas near male and spermathecal pores but present elsewhere in clitellar segments even though unrecognizable externally. Red clitellar coloration, as in other drawidas, in the epidermis.

Esophagus unusually short in the segment behind the last gizzard (as in most drawidas) and thence posteriorly wide, with thick wall bearing internally shortly papilliform to squarish protuberances, closely crowded in longitudinal or vertical rows. The vascular plexus appears in cross sections as a thick, dark red, uninterrupted layer. Valve, narrow, in hinder portion of xxi, anteriorly or posteriorly in xxii. In cross sections the plexus is represented by tiny red dots. In sections through the proximal portion of the intestine the red spots are larger and more closely crowded. Gizzards and valves, respectively, of eleven Rangoon worms are located as follows: xiv-xv and xxi-xxii (1, intestinal origin slightly behind 21/22); xiv-xvi, xxi (3, intestinal origin at 21/22 apparently); xiv-xvi, xxi-xxii (3, intestine beginning midsegmentally or posteriorly in xxii); xv-xvi (2, intestine beginning with 21/22 or midsegmentally in xxii); xv-xvii (2, intestine apparently beginning with 22/23). Commissures from extra-esophageals, in front of 8/9. Nephridia, present in x.

Vas deferens, very short, slightly sinuous in 9/10, looped around heart of ix and extra-esophageal trunk, almost straight in x, not especially thickened ectally. Prostates, 3-5 mm. long.

Spermathecal atria, 2-3 mm. long, ental half (approximately) widened, digitiform, ovoidal or ellipsoidal, abruptly marked off from stalk or more gradually narrowed in an ectal portion. Stalk wall thick, lumen narrow, more irregular entally.

Regeneration. Tail regenerate, 6 mm. long and with 40+ segments, at 65/66. Substrate length, 22 mm.

Remarks. Supposed variation in position of spermathecal pores relative to 7/8 is slight and may be fictitious, e.g., due to slight eversion from the spermathecal duct.

Intestinal origin was determined in Rangoon worms that had been anesthetized, pinned down straight, and then fixed. The esophagus was almost straight. Records of gizzard locations in worms listed above no longer are available.

TABLE 10

Location of genital markings in *D. papillifer peguana*

Locality	vii presetal	viii paired	Segments		vii median	viii
			viii postsetal	ix		
Naunggala (51)	6	9				
Taungzun (45)	7	14		3		
Kyauktan (14)	5					
Paukkaung (23)	10	6			2	
Thaton (32)	7	6				1
Wauetchaung (6)	6	2				
Magwe (26)						
Toungoo (4)					2	
Dam site (4)						
Ingabu (2)						
Labu (32)					5	
Kinmunsakhan (10)		1				
Pegu (4)				1		
Bilin (21)						
Pegu Yomas (22)		8		4	1	
Duyinzeik (22)	3	2				
Kungyangone (7)						
Twante (5)	1			2		
Kyaikto (13)		1				
Aungsaing (7)	1					
Tavoy district (12)			2			

DRAWIDA RANGOONENSIS Gates 1925

Sittang (Thaton), October, 0-1-3. K. John.

Kyauktan (Hanthawaddy), August, 0-0-2. K. John.

Rangoon (Hanthawaddy), various dates, 0-5-21. K. John.

Twante (Hanthawaddy), September, 0-7-9. K. John.

Pyapon, September, 0-2-1. Maung Ohn Maung.

Kyaiklat (Pyapon), September, 0-1-4. Maung Ohn Maung.

Maubin, October, 0-1-3. Maung Ohn Maung.

Bassein, October, 0-0-3. K. John.

Pegu, jungle to the east, August, 0-0-2. K. John.

Myohaung (Mandalay), September, 0-0-14. K. John.

Bhamo, September, 0-3-14. K. John.

Myitkyina, September, 0-7-3. K. John.

External characteristics. Nephropores, present from iii, in viii-ix usually slightly dorsal to *D*, apparently lacking in x. Clitellar coloration, sometimes lacking in *AA* of x-xi and more rarely of xii.

Spermathecal pores, very small transverse slits exactly on 7/8, margins usually smooth but not as straight as in *peguana*. Male pores, very small transverse slits, just in front of or more definitely anterior to 10/11, margins almost always slightly tumescent and often with an appearance of a thickly annular lip.

A transverse, slightly depressed, translucent area on each side of x is in the median half of *BC* and the equivalent of a setal annulus (secondary furrows lacking). The epidermis between that area and 10/11 is whitened and rarely with a diagonal or longitudinal central area of greyish translucence. Other paired genital markings usually are longitudinal but on viii and ix may be almost circular or more rarely transverse, in a middle or lateral portion of *BC* of x just lateral to translucent area, similarly positioned in ix but in viii more lateral and often just median to *C*, in viii-ix often in equivalents of setal annuli, in x-xi extending across equivalents of presetal and setal annuli and often reaching farther posteriorly, occasionally even to posterior intersegmental furrow. Median markings, usually between an intersegmental furrow and the equator, reach laterally to *A*, *B* or into *BC*. All markings except those in setal annulus of x are areas of slight epidermal thickening but without clitellar coloration.

Internal anatomy. Gizzards, 2-4, in xii-xvii (Table 12). Esophagus behind gizzards, usually distended by ingesta, rather sigmoid, on the floor at mV one or two longitudinal lamelliform ridges, or a horizontal band marked off into 2-4 sections. The

vascular plexus is much thicker, except just behind last gizzard and in the valve, than in the intestine. Gizzards and intestinal origin, respectively, of Rangoon specimens: xiii-xv, immediately behind 22/23 (3); xiv-xvi, midsegmentally in xxiii (1) or immediately behind 23/24 (5); xv-xvii, immediately behind 24/25 (1).

Commissures from extra-esophageals, in front of 8/9. The hearts of viii unite above the esophagus to open into dorsal trunk through a single short vertical vessel in median plane. Nephridia, of x lacking (10 adults).

Was deferens, slender and iridescent entally, passing ventrally median to the heart and then looped around the heart of ix, after passing into x in several hairpin loops (not always easy to find), then thickened and in a cluster of loops that may be nearly as large as or larger than the testis sac. Prostates, 1.0-1.5 mm. long, capsule slightly widened entally.

Spermathecal atria, 3-5 mm. long, saccular rather pear-shaped. A short ental portion of the sac occasionally is invaginated into the atrial lumen. Spermatozoal iridescence, slight, has been noted (several specimens) in atria as well as ampullae.

Remarks. Nephropores of ix and xi often are difficult to identify though probable sites are recognizable even when patent apertures were not seen. A more or less pore-like marking occasionally visible near *D* of x presumably marks site of a nephropore that was functional in juveniles stages.

TABLE 11
Location of genital markings in *D. rangoonensis*

Locality	Segments				Segments			
	viii	ix	x	xi	viii	ix	x	xii
	Paired				Median			
Rangoon	26	26	26	26		1		1
Kyauktan	2	2	2	2			2	
Pyapon	2	2	3	3				1
Myohaung	6	6	14	14	3			1
Kyaiklat	4	4	5	5	1			
Pegu			2	2	1			
Bassein	3	3	3	3			1	
Maubin	4	4	4	4				
Twante	11	13	16	16			2	3
Sittang	2	3	3	3				3

Median markings of viii-ix and xii-xiii are postsetal, but in x are presetal. Paired markings are in *BC*.

TABLE 12

Frequency distribution of segmental position and number of gizzards in *D. rangoonensis*

Locality	Segments						Number of gizzards		
	xii	xiii	xiv	xv	xvi	xvii	2	3	4
Twante (6)	1	4	5	6	3	1		4	2
Maubin (4)		3	4	4			1	3	
Pyapon (3)		3	3	3				3	
Kyaiklat (2)		2	2	2				2	
Sittang (1)		1	1	1				1	
Kyauktan (2)		2	2	2	1			1	1
Bassein (3)		1	3	3	3	1		1	2
Rangoon (14)		8	13	14	12	1	1	6	7
Totals	1	24	33	35	19	3	2	21	12

DRAWIDA RARA Gates 1925

Kamaungthwe River (Tavoy), September, 0-2-0. W. D. Sutton.
Moulmein (Amherst), August, 0-3-6. October, 0-2-1. K. John.
Mupun (Amherst), October, 0-26-18. K. John.
Thaton, September, 0-14-20. K. John.
Duyinzeik (Thaton), September, 0-7-0. K. John.
Naunggala (Thaton), September, 0-0-3. K. John.
Bilin (Thaton), September, 0-4-0. K. John.
Aungsaing (Thaton), September, 0-8-5. K. John.
Sittang (Thaton), October, 0-13-1. K. John.
Syriam (Hanthawaddy), September, 0-9-5. K. John.
Rangoon (Hanthawaddy), various dates, 0-39-36. K. John.
Kungyangone (Hanthawaddy), September, 0-2-0. K. John.
Dedaye (Pyapon), September, 0-1-0. Maung Ohn Maung.
Bassein, October, 0-15-18. K. John.
Danubyu (Maubin), October, 0-2-0. Maung Ohn Maung.
Hlawga (Insein), September, 0-3-0. K. John.
Taukkyan (Insein), September, 0-3-1. K. John.
Hmawbi (Insein), September, 0-10-5. K. John.
Wanetchaung (Insein), September, 0-18-3. K. John.
Taikkyi (Insein), September, 0-23-14. K. John.
Dam Site (Insein), September, 0-44-2. K. John.
Pegu, August, 0-16-10. Jungle to the west, 0-14-4. Jungle to the east,
0-13-10. K. John.
Thayetmyo, September, 0-2-0. K. John.
Allanmyo (Thayetmyo), September, 0-2-0. K. John.
Pyinmana (Yamethin), October, 0-8-0. K. John.
Taungdwingyi (Magwe), August, 0-23-18. K. John.
Magwe, August, 0-4-6. K. John.
Minbu, August, 0-2-2. K. John.
Myohaung (Mandalay), September, 0-1-4. K. John.

Wuntho (Katha), hills to the west, September, 0-0-1. Saw San Thwe.
Myitkyina, September, 0-18-14. K. John.

External characteristics. Length, 35-50 mm. (Taungdwingyi, Aungsaing and Magwe). Nephropores, present from iii, close to *D* in viii-ix, apparently always lacking in x. Clitellar coloration, red, often lacking ventrally in x and a presetal portion or all of xi, the uncolored area often delimited by slightly irregular longitudinal furrows at level of lateral margins of male porophores.

Spermathecal and male pores, larger than nephropores and certainly larger than female apertures, transversely slit-like. Spermathecal pores, at or just median to *C*, each usually surrounded by an annular lip, the pore apparently located on posterior margin of vii, the lip when specially swollen with an appearance of a short transverse papilla. Rarely, a posterior portion or even all of the lip is lacking and then the pore appears to be on 7/8. The tumescence is believed to be an everted portion of the spermathecal duct.

Genital markings: paired and nearly circular, pre- and postsetal in *BC* of x, transverse and in setal annuli of x and xi just lateral to *B*; unpaired, presetal and postsetal in *BB* (or reaching slightly into *BC*) of viii, x-xi. Markings in setal annuli often are slightly smaller than other paired markings, greyish translucent rather than white, depressed rather than protuberant and without epidermal thickening. Paired markings occasionally present in *BC* of viii (pre- and postsetal) or vii (postsetal) are transverse, indistinctly demarcated areas of epidermal thickening. Paired postsetal markings usually (Pyinmana, Taungdwingyi, Minbu, Magwe, Allannyo, Thatyetmyo) are lacking in x.

Internal anatomy. Gizzards, 2-4, in xii-xviii (Table 13). A midventral, typhlosole-like ridge is present in the gut behind the gizzards but may not be as obvious as in *rangoonensis*. Location of gizzards and intestinal origin, respectively, in several Rangoon specimens: xiv-xvi, midsegmentally in xxii (3) or just behind 22/23 (2); xv-xvii, just behind 22/23 (4) or midsegmentally in xxiii (12) or just in front of 23/24 (1) or just behind 23/24 (2); xv-xviii, midsegmentally in xxiii (2); xvi-xvii, just behind 22/23 (1) or midsegmentally in xxiii (1) or just behind 23/24 (2); xvi-xviii, just in front of 23/24 (1) or just behind 23/24 (6). The intestine begins, in a Taungdwingyi worm with gizzards in xiv-xvi, just behind 21/22. Commissures from extra-esophageals, in front of 8/9.

Vas deferens, short, slender, with several loops in 9/10 and on anterior face of 9/10, twisted around hearts of ix, with several further loops on posterior face of 9/10 in a small compact cluster, an ectal portion only slightly thickened.

Abnormality. (No. 1.) Right spermathecal duct, about half way down to parietes, passes into vii where a short portion is widened into a thin-walled vesicle. (No. 2.) Right male porophore entirely in x and extending from the presetal secondary furrow nearly to 10/11. The male pore is about midway between eq/x and 10/11. (No. 3.) Testis sac, vas deferens, prostate, male pore and porophore as well as genital markings of left side, lacking.

Regeneration. Tail regenerates, of 28+ segments at 72/73 and of 26+ segments at 81/82. Lengths of substrates and regenerates, respectively, 28 and 4, 31 and 5 mm.

Remarks. Male porophores of four Taikkyi worms are represented only by circular areas of epidermal whitening, distinctly demarcated but not protuberant. The pores are transversely placed slits at 10/11 which appear to be nearly as deep across the porophore as elsewhere. Prostates of these specimens are unusually high in the coelomic cavity though capsules still are almost confined to the parietes.

Male porophores in *rara* seem incapable of marked elevation. However, by bringing the prostatic capsule deeper into the parietes, a small part of the porophore containing the male aperture can be raised into a teat-like protuberance presumably for insertion into the spermathecal pore. The lumen in the thickened portion of the spermathecal duct may be large enough to receive the protuberance. Entrance perhaps is facilitated by slight eversion of the duct.

The unusually small size of the prostatic capsule presumably is secondary rather than primitive but in either case distinguishes *rara* from *constricta* Gates 1929. Connectives from the extra-esophageal trunks are on opposite sides of septum 8/9 in the two species. Discoidal male porophores extending into x and xi have been developed in both species but seem capable of greater elevation (as temporary intromittent organs) in *constricta*. Genital markings of both species are similar to those of *spissata* Gates 1930 where they also are not associated with definite glands. The male pores of *spissata* certainly do appear to be well inside xi but all specimens had protruded porophores (discoidal on relaxation and restricted to xi?). Assuming that adiverticulate

spermathecae are evidence, in Burma, of phylogenetic relationships, *spissata* can be derived from a common ancestor of *rara* and *constricta* by the following changes: migration of male pores back into xi, increase in number of gizzards (now apparently 4-5), elongation of esophagus so as to place the gizzards farther posteriorly, elongation of prostates as well as male deferent and spermathecal ducts. Additionally, the spermathecal ducts have been thickly muscularized, especially so in the ectal 35-50 mm., and the vasa deferentia (in x only) have been thickened.

TABLE 13

Frequency distribution of segmental position and number of gizzards in *D. rara*

Locality	Segments							Number of gizzards		
	xii	xiii	xiv	xv	xvi	xvii	xviii	2	3	4
Magwe (15)	1	12	15	15	9				8	7
Wuntho (2)		1	1	2	2			1		1
Taungdwingyi (6)		1	5	6	4			2	4	
Thaton (11)		1	11	11	11	8			2	9
Pegu (22)		6	17	22	22	14	2		5	17
Mupun (15)		2	12	15	15	10	2		4	11
Myohaung (5)			4	5	5	1			5	
Taikkyi (5)			4	5	5	1	1		4	1
Rangoon (9)			1	9	9	6	2	2	5	2
Bassein (2)				2	2	2	2			2
Syriam (2)				2	2	2	2			2
Totals	1	23	70	94	86	44	11	5	37	52

DRAWIDA TENELLULA nom. nov.

1933. *Drawida* sp., Gates, Rec. Indian Mus., 35:476.

Remarks. Ovisacs were small in both specimens (acitellate) but other genital organs probably were fully developed.

The "penes," if definite structures, presumably are retractile into chambers possibly restricted to the parietes. Otherwise, the penes could be produced perhaps by eversion of the prostatic duct. In either case complete retraction is likely to leave a fairly large secondary male pore that would provide an additional distinction from the various species mentioned below. Protrusion of a discoidal porophore in a tubular fashion now seems unlikely and is contra-indicated by texture of penial epidermis.

D. tenellula is distinguishable from *bullata* by the penis-like male porophores and absence of definite genital markings. From

other species with shortly digitiform spermathecal atria *D. tenellula* is further distinguished as follows. From *D. vulgaris* by the longer vas deferens. From *D. gracilis* by the much smaller size, smaller ventral setae of iii-vii, erect prostates, thickening of the vas in xi, peripheral closure of ovarian chamber. From *D. flexa* by the longer vasa deferentia and absence of special parietal glands associated with genital markings.

DRAWIDA VICTORIANA n. sp.

Mount Victoria (Pakokku Chin Hills), on east side near path from Kaupetlet to summit, at 3000 feet, in teak forest and grass land, July, 0-1-0.
G. Heinrich.

External characteristics. Length, 64 mm. Diameter, 3 mm. Setae, unrecognizable or almost so in an anterior portion of the body, posteriorly $AA < BC$, AB slightly $< CD$. Nephropores, present from iii, at or close to *D*.

Spermathecal apertures, probably at $7/8$ and at or just median to *C*. Male pores, in *x* and very slightly lateral to *B*, very small, transverse slits at tips of anteriorly directed, rather conical protuberances from posterior margin of *x*. Porophores are in slight depressions where the epidermis is whitened, smooth and glistening.

Genital markings, small, median and postsetal in vii-xi, paired, in *BC* and about in line with male porophores, in presetal and also in setal annulus of *x*, in postsetal annulus of *xi*. A smaller presetal marking is present in lateral portion of *AA* in *x*. Each marking, except in vii, nearly circular, with a distinctly demarcated rim and a longitudinal or transverse area of greyish translucence centrally.

Internal anatomy. Septa, $5/6-8/9$ muscular. Gizzards, four, in xvi-xix. Commissures from extra-esophageals, in front of $8/9$.

Testis sacs, dislocated posteriorly behind the ovarian chamber. Vas deferens, slender and iridescent entally in $9/10$ and in *ix* near hearts, a preseptal portion in *ix* 5-10 mm. long and in a small cluster of u-shaped loops, the postseptal portion thickened and in a cluster of loops that is as large as or larger than the testis sac, passing directly into prostate just below its ental end. Prostates, rather slenderly club-shaped, $2\frac{1}{2}$ mm. long, nearly straight or bent into a u-shape, capsule slenderly club-shaped and nearly circular in cross section.

Spermathecal duct, slender, slightly zig-zag looped as it passes ectally on posterior face of 7/8. Atrium, saccular, large, erect in vii and in contact with dorsal parietes, the ectal half stalk-like. Annular ridges are present on inner wall of stalk and sac. Ovarian chamber, probably closed off from parietes. Ovisacs, in xii-xiv or xv.

Longitudinal musculature, uninterrupted over sites of genital markings.

Remarks. Pigment was not recognized and may be lacking but the body wall had been deeply stained by some post-mortem accident. The anterior end was distorted probably as a result of local desiccation.

Yolk was present only in a posterior portion of partially collapsed ovisacs, a condition that is suggestive of an early post-sexual stage. The glandular investment of the prostates, thin and firmly adherent to the capsule, is more like conditions of a presexual stage.

Genital markings of the kind present on the type, in other species usually are associated with small solid glands having transparent walls. If such glands are present, *victoriana* is distinguished from *papillifer* and *nagana* by the protuberance of the male porophores and from *nepalensis* by location of male pores in x as well as by characters of the porophores. If glands are absent, *victoriana* is distinguished from *rangoonensis* by the protrusibility of the male porophores and from *moesta* by absence of penes. To permit entry in a key, glands are assumed to be present.

Reproduction. Iridescence in an ental portion of the male gonoducts shows that sperm had been matured. A similar iridescence in the coagulum of an ectal portion of the atrial stalk shows that sperm had been received, presumably from another worm. Reproduction, accordingly, is assumed to be sexual and biparental. (No iridescence was recognizable in the coagulum within the spermathecal ampulla.)

Regeneration. A tail regenerate is 3 mm. long.

DRAWIDA VULGARIS Gates 1930

Prome, September, 0-2-12. K. John.

Paukkaung (Prome), September, 0-18-20. K. John.

Mt. Popa (Myingyan), September, 0-0-2. K. John.

External characteristics. Length, to 50 mm. Diameter, $2\frac{1}{2}$ -3 mm. Nephropores, present from iii, in or close to CD, apparently

lacking in x. Setae, *AA* usually $< BC$ but on some Paukkaung worms may = *BC*, *DD* ca. = $\frac{1}{2}C$.

Male pores, small transverse slits on posterior margin of x, at or slightly median to *mBC*, with or without an obvious though small, annular lip. A posterior portion of x bearing the male pore may be protuberant as on the types or not. In the latter case the male pore is concealed from view by the anterior margin of xi.

Genital markings, transverse, shortly elliptical, presetal, opaque areas, each with a greyish translucent center, in Paukkaung worms indistinctly delimited and recognizable only in best optical conditions. Paired markings usually are in a lateral portion of *BC*, with centers slightly lateral to levels of male pores. A pair of whitened patches usually slightly nearer *B* on each of the present worms extends from 10/11 to postsetal secondary furrow of x. In one or the other of those patches there occasionally is recognizable a typical marking with central translucence. Markings apparently are lacking on the Popa worms. The markings of Paukkaung and Prome worms, respectively, are as follows: in ix (38 and 12 specimens), in x (38 and 12); median, in *AA*, of viii (1 and 5); of ix (17 and 9); of x (0 and 4); of xi (19 and 7); of xii (14 and 6); of xiii (1 and 0).

Internal anatomy. Gizzards, two to four in xii-xvi, xii-xiv (3 Prome), xii-xv (1 Paukkaung), xiii-xiv (1 Paukkaung, 2 Prome), xiii-xv (4 Paukkaung, 2 Prome), xiv-xvi (1 Popa). Commissures from extra-esophageals, in front of 8/9. Posterior commissures from extra-esophageals pass into hearts of ix just lateral to median plane. Hearts of ix unite mesially just above gut and are then connected with the dorsal trunk by a short, vertical vessel in the median plane. A vessel from the posterior commissures of the extra-esophageals passes posteriorly on dorsolateral face of the gut to xii or xi. Nephridia of x, lacking.

Testis sacs, usually laterally flattened, equally in ix and x, rather reniform to shortly u-shaped, concave ventrally, more or less deeply constricted by 9/10. Vas deferens, slender and iridescent entally, passing into ix median to the heart, then anterior to the heart and back to 9/10 where it is twisted into several short loops, the portion in x thickened and opaque, also twisted into several loops, then passing directly into the prostate. The vas of one Prome worm is about 8 mm. long, length of the slender portion just over 3 mm. Prostatic capsule, about one mm. long, slenderly rod-like but with some slight ental widening,

soft, opaque, of about the same thickness as the glandular investment.

Spermathecal atria, always in vii, about one mm. long.

Remarks. Differences from *bullata* are few but apparently constant in a range that extends into Thailand. Vasa deferentia of all specimens referred to *vulgaris*, like the spermathecal atria, have been short as in the smallest specimens of *bullata*. Male pores of *bullata* always were in or appeared to be in xi. In *vulgaris*, however, the male pores always were in or appeared to be in x.

TABLE 14
Location of genital markings in *D. vulgaris*

Locality	Segments							
	ix	x	viii	ix	x	xi	xii	xiii
	Paired					Median		
Paukkaung	38	38	1	17	—	19	14	1
Prome	12	12	5	9	4	7	6	—

Paired markings are located laterally in BC. Median markings are confined to 4A.

TABLE 15
Frequency distribution of segmental position and number of gizzards in *D. vulgaris*

Locality	Segments					Number of gizzards		
	xii	xiii	xiv	xv	xvi	2	3	4
Prome (6)	3	7	7	2		1	4	1
Paukkaung (7)	1	6	6	5		2	5	
Mt. Popa (1)			1	1	1		1	
Totals	4	13	14	8	1	3	10	1

Genus MONILIGASTER Perrier 1872
MONILIGASTER CERNOSVITOVİ nom. nov.

1940. *Moniligaster beddardi* Gates, Rec. Indian Mus., 42:496. (Type locality, Kodaikanal. Types in the Indian Mus.)

M. beddardi Gates 1940 is preoccupied by *M. beddardii* Rosa 1890 now *Drawida beddardi*, and would have been renamed long ago had there been any occasion to refer to the genus.

MONILIGASTRID PHYLOGENY

The numerous differences from most earthworms suggest long separation of moniligastrid stocks from other lines of megadrile

evolution. Unless peculiar characteristics, in identical combinations, evolved independently in the ancestry of each genus, an early moniligastrid should have differed from contemporaneous oligochaetes as follows: prostomium, now independent of the peristomium and attached to the roof of the buccal cavity behind level of intersegmental furrow $1/2$; digestive system, with enterosegmental organs, with esophagus elongated posteriorly so that the gizzard is behind the ovarian segment, perhaps with intestinal origin at first in xv where it still is today in many megadriles; vaseular system, with paired extra-esophageal trunks that are lateral to the hearts, with a parietal subneural trunk, one or two pairs of hearts at posterior end of the series united dorsomesially in each segment instead of opening into the dorsal vessel directly; testes, proliferating anteriorly into interior of their septa and no longer inducing development of seminal vesicles; ovarian chamber, closed off mesially from neural and esophageal portions of the coelom; spermathecae, deeply invaginated into the coelom so that ampullae are dorsal; capsular genital glands, evolved from the X glands. While so much typically moniligastrid anatomy was being evolved, gonads of the ancestral battery may well have been eliminated in all but four segments, x-xiv.

Ancstral characters still retained were as follows: genital apertures, of all organs from spermathecae to glands, minute, superficial, in the ventrum; spermathecal, male and female pores in region of *AB*; gland pores variously located in *BB*; sigmoid setae, in four pairs of longitudinal ranks; clitellum, unilayered; gonoducts short, and opening directly to the exterior in presetal portions of the segments; hearts, lateral (a supra-esophageal trunk still lacking); ovisacs, dorsal and posteriorly elongated; gizzard, still esophageal and single; nephridial ducts, passing straight through the parietes. Pigment may have been lacking.

An important early change in moniligastrid anatomy resulted from acquisition by genital glands of ability to attract toward and into themselves during early growth the elongating male gonoducts. At first gonoducts may have joined, regardless of location, the nearest glands, or if several were equidistant those that were growing faster or had invaginated earlier. Eventually stabilization was achieved and the vasa deferentia joined only those glands developing at the intersegmental level next behind that of the gonad septum. Henceforth, male gonoducts were to be unable to open to the exterior in absence of prostates.

Reduction in the gonad battery was continued. In a line leading to *Desmogaster*, gonads of x were aborted and those of xii became testes. In lines leading to *Hastirogaster* and *Eupolygaster*, gonads of x and xii, of x and xiii, respectively, were eliminated. In the main line leading to *Drawida-Moniligaster*, gonads of xii-xiii disappeared (unless a segment was exelated anteriorly), those of xi being retained as ovaries. Other reductions and modifications in the battery would seem to have been possible. If so, additional genera may be found in unexplored portions of the moniligastroid domain east of Burma.

Development of additional hearts at posterior end of an ancestral series appears to have been limited by location of the ovarian chamber as none have appeared behind a level two segments in front of that chamber. Thus, the last hearts of drawidas are in ix but of desmogasters are in xi. One pair of spermathecae was eliminated in the ancestry of *Drawida* (and *Hastirogaster*?) but elsewhere the reduction has been intragenerie.

Subsequent to appearance of extant genera, known macroscopic changes have been confined almost entirely to short portions of nephridial ducts, a section of the gut behind the ovarian segment and, of course, to the genital system. Parietal portions of nephridial ducts now may grow laterally as well as mesially within the body wall to acquire at several levels external openings, often irregularly placed and with more or less asymmetry. The esophagus has been further elongated. Esophageal gizzards (cf. Tables 16-17) have been multiplied and moved posteriorly. Body size has been increased sufficiently, in various countries, to warrant the characterization of "giant earthworms." These somatic modifications now appear to have been made independently in various genera.

Among independently made changes in the genital system are: lateral dislocations of male and spermathecal pores; closure of the ovarian chamber from the parietes; elongation of spermathecal and male ducts; development of intromittent organs; various modifications in shape of the prostatic capsule as well as reduction (and final elimination?) of the glandular investment.

Female pores have remained in their primitive position throughout the family, and spermathecae still are adiverticulate except in various lineages of *Drawida*. Although more information is available for that genus than for all others it is not yet sufficient to allow more than a tentative indication of relationships and changes in a few small groups.

A rather primitive *willsi* species group has retained prostatic-like (GM) glands but has acquired pigment. Spermathecae still are adiverticulate in the Assamese *limella* Gates, 1934, but pores are at mBC, gizzards are three in xiii-xv and the prostatic capsule has become so small that it is almost confined to the parietes. Genital apertures still are at or close to B in species of peninsular India which now have spermathecal atria. *D. scandens* Rao, 1921, with prostates and GM glands of the same size, has two or three gizzards in xii-xv. *D. dolosa* Gates, 1945, with two to four gizzards in xiii-xvi, has shortened prostates that may be only a quarter as long as the GM glands. *D. periodiosa* Gates, 1934, with two or three gizzards in xiii-xvi has prostatic capsules so small as to be almost confined to the body wall. *D. willsi* Michaelsen, 1907, with two to four gizzards in xii-xvi, has GM glands that are shorter and slenderer than the prostates. Occasional individuals have no glands.

All Burmese species have spermathecal pores at or close to C and a region around site of each primary male pore usually is modified to some sort of a porophore for more efficient transfer of sperm during copulation.

A *beddardi* group, probably with a peripherally closed ovarian chamber, lacks pigment and spermathecal diverticula though a terminal portion of the spermathecal duct is thickened. *D. delicata*, with four gizzards in xii-xv, has markedly lengthened male gonoducts but spermathecal ducts still are short. *D. kempi* Stephenson, 1914, with gizzards in xv-xix, has spheroidal prostatic capsules. *D. rara*, with three to five gizzards, in xii-xviii, has prostatic capsules that are vestigial and confined to the parietes. *D. constricta*, probably close to *rara* but with only two or three gizzards in xiv-xviii, has less shortened prostatic capsules that still reach into coelomic cavities. *D. spissata* Gates, 1930, with four or five gizzards in xvii-xxi, has much lengthened prostates, vasa deferentia and spermathecal ducts, the latter markedly muscularized ectally. *D. beddardi*, with three or four gizzards in xii-xix, still has digitiform prostatic capsules but with the glandular investment occasionally restricted to small ental portions. Male pores have been invaginated and now are on tubular penes pendent from roofs of eversible, muscular-walled chambers more or less protuberant into the coelom.

Possibly derived from a distant ancestor of the *beddardi* group is *caerulea*, with pigment, male pores deeply invaginated

into muscular copulatory chambers that have no glandular investment and contain no penes. Spermathecae, in the southern portion of the range, still are adiverticulate though the terminal thickening of the duct may be slightly larger than in the *beddardi* group. A muscularized atrial outgrowth of the thickened portion of the duct has appeared in more northern forms and still farther north has reached septum 6/7 and the dorsal parietes. Elongations already under way in the north have become even greater in the Assamese *deccourcyi* with atria, spermathecal and male ducts, respectively, reaching lengths of 8, 20 and 650 mm. Gizzards, still only 1 or 2 in xiii-xvi of a central Burma population, in *deccourcyi* now are 7-9 in xiv-xxvii.

Other Burmese species, all with diverticulate spermathecae, appear to belong in two groups of more or less closely related forms distinguished by presence or absence of definite glands (not prostate-like) in association with the genital markings. One section of the glandless group has digitiform spermathecal atria. Three species still have digitiform prostatic capsules: *D. vulgaris*, with 2-4 gizzards in xii-xvi, short atria and vasa deferentia; *D. tenellula*, with 3-4 gizzards in xiii-xviii, and lengthened vasa; *D. bullata*, with 1-5 gizzards in xiii-xviii, atria and vasa that vary from short to considerably elongated. *D. gracilis*, with 1-4 gizzards in xiv-xxi, short atria, lengthened vasa but prostatic capsules that reach into coelom only slightly. *D. lacertosa*, with 3-5 gizzards in xiii-xx, short but muscularized spermathecal ducts and atria, has lengthened vasa, anteroposteriorly elongated and bilobed prostatic capsules sessile on the parietes.

An ental portion of the somewhat elongated spermathecal atria, in the second section of the glandless group, has become a thin-walled sac. *D. rangoonensis*, with 2-4 gizzards in xii-xvii, has elongated vasa but nearly digitiform prostatic capsules. *D. molesta*, with 3-5 gizzards in xiii-xxi, elongated vasa and prostatic capsules, has invaginate male pores on tubular penes.

GM glands of the remaining group are solid and bear on their outer faces part or all of a more or less distinctly delimited genital marking. Most species have digitiform atria. Two of the species in that section have clear glands with transparent or translucent walls. *D. assamensis*, with 4-5 gizzards in xii-xvii, has short spermathecal ducts, atria, vasa deferentia and prostatic capsules. *D. flexa*, in peninsular Burma, also has short atria and vasa but the gizzards (4-5) are in xvi-xxiv and glands are much more numerous. *D. nana*, with 2-3 gizzards in xiii-xv, has

TABLE 16
Frequency distribution of gizzard number and of segmental position in *Dravida longatria* and closely related species.

Number of gizzards		Locality	Segments											
26	30	Sagaing	1	19	55	51	16							
13	42	Tonbo-Kyaukkyone	2	23	44	50	31	6						
43	12	Kaungmudaw		1	15	56	49	5						
2	28	Thazi		4	15	34	38	21						
28	33	Mandalay-Tonbo		2	15	40	54	36	8					
	8	Maubin			1	6	10	10	5					
1	12	Rangoon			6	27	29	26	16	3				
9	38	Bassein-Kokya-Kochi			8	30	48	42	22	2				
3	8	Yamethin			1	9	16	16	13	3				
1	16	Tharrawaddy			1	5	13	26	26	17	2			
	6	Tavoy	2		8	70	114	136	134	79	21	1		
	28	Sadoway				8	32	35	31	6				
1	30	Pyapon				9	31	39	34	10	2			
	3	Blachi-Leiktho				2	8	9	9	6				
	3	Chaungson				2	3	8	10	9	6			
	2	Shwegyin-Paung						5	9	10	11	7	1	
6	87	<i>D. tumida</i>	31			10	77	116	124	119	67	8		
10	80	<i>D. flexa</i>	10			2	34	80	98	105	87	29	8	2

TABLE 17

Frequency distribution of segmental position and of gizzard number in other species of *Drawida*.

Segments												Number of gizzards						Species
12	13	14	15	16	17	18	19	20	21	1	2	3	4	5	6			
18	48	53	39	4							6	38	9			<i>vulgaris</i>		
26	91	99	50	10							29	66	5			<i>willsi</i>		
14	77	116	117	64	7						9	71	41			<i>edalebi</i>		
5	54	97	100	70	3						3	65	32			<i>rangoonensis</i>		
4	50	177	266	255	163	33					5	135	127	5		<i>rara</i>		
1	5	56	98	98	63	23	4				6	66	32	2		<i>papillifer peguana</i>		
	13	59	94	71	25	6					52	48	5			<i>caerulea caerulea</i>		
	6	31	44	44	38	19	2					6	24	14		<i>f. abseisa</i>		
	1	16	38	49	48	35	7					8	34	6	1	<i>lacertosa sepulta</i>		
	1	12	58	64	54	26	3	1			9	39	21			<i>papillifer papillifer</i>		
		8	21	33	41	30	19	4	2	1	10	35	8			<i>gracilis</i>		
					12	12	12	12	2				10	2		<i>spissata</i>		

glands with opaque but soft walls. Vasa, atria, possibly spermathecal ducts and prostates, are lengthened. The rest of the species in the section have glands with thickly muscular walls. *D. tumida*, with 3-5 gizzards in xvi-xxii, has short atria but vasa are somewhat elongated. *D. longatria*, with 1-6 gizzards in xiii-xxiii, has spermathecal atria 2-180 mm. long. Male gonoducts are of similar variable lengths.

An ental portion of the somewhat elongated spermathecal atria has become a thin-walled sac in other Burmese species which have almost digitiform prostatic capsules and (one exception?) clear glands. *D. papillifer*, with 2-5 gizzards in xii-xx still has short vasa, no protuberant male porophores and an ovarian chamber that is not closed off from the parietes. Pigment, possibly similar to that of *caerulea*, is present. *D. nepalensis* and *victoriana*, with gizzards in xii-xxiii and xvi-xx, respectively, now have elongated vasa, protrusible male porophores and an ovarian chamber closed off from the parietes.

OLIGOCHAETE PHYLOGENY

The supposedly Jurassic or Cretaceous ancestor of the megadriles usually was believed to be octogonadal, with testes in x-xi and ovaries in xii-xiii. Divergent conditions in modern earthworms, except moniligastrids, resulted from elimination of the anterior ovaries and, less frequently, of the first or second pair of testes. The phylogenetic puzzle posed by the Moniligastridae required answers to several questions among which were the following: 1) How had testes of x-xi gotten into xi-xii during evolution of *Desmogaster* from the supposedly ancestral haplotaxid? 2) How did ovaries of xiii get into xi as *Drawida*³ was evolving from *Desmogaster*? 3) At the same time, how did one pair of desmogaster testes, either from xi or from xii, get into x? 4) How had male gonoduct funnels gotten from one septum into sacs of the preceding septum?

Evolution of gonadal batteries within the Moniligastridae requires "some possibility of the intercalation or excalation of segments" according to Beddard (1891) who offered no suggestions as to how the deletions or insertions could have been brought about. The only attempt at a solution of the moniligastrid puzzle is Stephenson's ingenious "contraction" theory which Avel

³ *Drawida* is understood, in most of this discussion, to include *Moniligaster*. The genera are so much alike that Michaelsen seems to have repented separating them. *Moniligaster* may be only an unusually distinct species group.

(1959) deems plausible. Michaelsen, however, appears to have been unwilling to approve — except for mention of several difficulties in a footnote (1922), he continued to ignore the problem which certainly was involved in his own derivation of the Moniligastridae from the Haplotaxidae.

If moniligastrid testis sacs, as Beddard suggested, are vestigial coeloms of segments from which all parts except gonads, gonoducts and their funnels have disappeared, it should be possible to determine the ancestral condition by “expanding” the sacs to their original metameric state. The genera thus theoretically treated by Stephenson are *Syngenodrilus* and *Desmogaster*. Results were identical, testes in xii as well as x and ovaries in xiv (for figures cf. Stephenson, 1922 or 1930). Then, to restore the primitive continuity of the series, testes were inserted in xi and ovaries in xiii thus providing a decagonadal battery. Conditions in most megadriles resulted from elimination of gonads in xiv, xii and x or xi but in moniligastrids resulted from partial or complete abortion of gonad segments. Contraction of the tenth and twelfth segments to testis sacs along with elimination of testes in xi and of ovaries in xiii produced *Desmogaster*. Fusion of desmogaster testis sacs and elimination of an intervening segment to bring testes of x into association with male funnels formerly in xii, gave *Drawida*.

Various sorts of evidence, including some from *Syngenodrilus*, were cited in support of the contraction theory. 1) The epithelium lining the moniligastrid testis sacs requires the cavity of the sac to be coelomic. 2) Trabeculae, within the sac, were thought to be remnants of former septa. 3) The ovarian chamber of various moniligastrids has only to be separated into discrete halves along with loss of nephridia to reproduce identically the testis sac condition. 4) Similar contractions are said to be under way in various megadrile families.

Although Michaelsen's criticisms now appear unimportant, contraction still is unacceptable and for the following reasons. 1) Expansion of *Syngenodrilus* testis sacs involved misinterpretation of figures and text of an inadequate and, in part, erroneous characterization of the type species. Independent examinations of the type (Gates 1945, and Pickford, 1945) found testis sacs to be membranous enclosures of small portions of coelomic cavities. These sacs are in no way comparable to the so-called testis sacs of moniligastrids and there had been no reduction in size of testis segments. 2) *Desmogaster* gonads

were assumed to be one segment in front of the locations mentioned in the literature. Subsequent investigations have confirmed the original records. 3) Evolution of the moniligastrid ovarian chamber has involved no reduction in size of the ovarian metamere. Essentially, all that has happened is a partitioning off from the rest of the coelomic cavity of a portion containing the ovaries, nephridia and oviduct funnels. Halving the sac and eliminating nephridia would leave size of ovarian segment unchanged and would not provide sacs homologous with those containing the testes. 4) Similarly, supposed contractions in *Acanthodrilus*, *Hoplochaetella* and *Eutyphoeus*, as well as various changes in other genera, all involve subdivision of coelomic cavities but always without any real decrease in volume of coelomic space or in size of metameres. 5) Moniligastrid testis sacs (cf. p. 301) have no real cavity and no internal epithelium aside from the male funnel. Trabeculae are only muscle strands without peritoneal covering.

The moniligastrid problem was made unnecessarily difficult by the phylogenetically-based classical system in which *Drawida* is directly descended from *Desmogaster*. If *Eohippus* could not remain *Eohippus* during all of the time it was evolving into *Equus*, *Desmogaster* is unlikely to have remained *Desmogaster* while evolving into *Drawida*. Hence *Drawida* ovaries of xi and *Desmogaster* testes of xii, as well as other aspects of the puzzle, can be considered separately and independently rather than simultaneously.

The *Drawida* condition can be derived theoretically from the ancestral octogonadal battery by elimination of the ovaries in xiii and the testes of x along with excalation of one segment in front of the gonad region. The gonads thus eliminated did disappear in evolution of the Enchytraeidae — if that family has a common ancestry with megadriles. The required excalation has been made (cf. below) in another family.

The *Desmogaster* condition cannot be derived by any of the evolutionary changes recognized in the classical system. Here also the problem was made unnecessarily difficult by an assumption of gonad immutability. Although never so stated, construction of the basic phylogeny proceeded as if the sexual nature of each gonad in the ancestral battery already had been irreversibly determined. Studies of parthenogenetic morphs by the author have shown that any testis can become hermaphroditic or even an ovary of different and distinctive shape. Determination of

gonads for maleness accordingly is reversible. Although that discovery is of no help in solving the *Desmogaster* problem, it does provide a second method of deriving the *Drawida* condition from the octogonadal battery, viz., by elimination of gonads in xii and xiii along with conversion of testes in xi to ovaries. Conversion of ovaries to testes has not been found in the author's morphs and is not to be expected in series hitherto studied, as oligochaetes seem to have an innate prohibition against evolution of dioecism.⁴ The literature does, however, contain various records of gonads in xii of normally metagynous species — those in which the gonads of xii usually abort ontogenetically. Unaborted gonads of xii in such individuals were ovaries, hermaphroditic, or even testes. The *Desmogaster* condition then can be derived merely by eliminating from the ancestral octogonadal battery the testes in x and by conversion of ovaries in xii to testes.

Gonadal batteries of two megascolecid genera, *Tonoscolex* and *Nellosolex* Gates 1933 and 1939, with testes in ix-x and ovaries in xii, obviously can be derived only by excalation of one metamere in front of the gonad region. Fortunately, somatic as well as reproductive organs from the gizzard and posteriorly are one segment anterior to normal location. The excalated segment must then have been one of the first four or five. Just how the excision could have taken place is shown by changes now under way or recently made in various megadriles. The intersegmental furrow demarcating the first from the second segment, even when preservation is optimal, often is indistinct. That same furrow, along with the prostomium, has disappeared in *Pontoscolex corethrurus* (Müller, 1856) and the first two segments have become so small that together they are markedly shorter than the third. Actually, only presence of setae just in front of the first intersegmental furrow (originally 2/3) enables recognition of the fusion, just as in the apparent peristomium of the leech-like oligochaete (cf. above p. 298), *Acanthobdella peledina* Grube, 1851, and in *Trichodrilus cantabrigiensis* (Beddard, 1908). Elimination of the setal follicles originally belonging in ii, that is now under way in various species, when completed will produce the elision required by *Tonoscolex* and *Nellosolex*.

Also noteworthy in the same connection is the derogation of metameric organization anteriorly that has become common, presumably subsequent to retraction of the brain into the region of

⁴ All supposed cases of dioecism now have been found to be instances of genital polymorphism in which the morphs have evolved after establishment of parthenogenesis.

segment iii and of the united cord ganglia of i-iii to a slightly more posterior level. Among those long known "cephalizations" are various abortions, presumably often ontogenetic: of setal follicles in ii as well, sometimes, as several successive segments; of portions or all of one or more of septa 1/2-4/5; of nephridia in ii or occasionally even in additional segments as far back as x-xiv; of parts or all of vascular commissures between dorsal and ventral trunks in ii-iv or v, of the dorsal trunk itself and back to hearts of vi, vii, viii or even ix.

Excalation of one segment, along with elimination from the octogonadal battery of one pair of ovaries and/or one pair of testes provides gonadal conditions in most microdriles. Two exceptional lumbriculid genera, *Styloscolex* and *Premnodrilus*, require two segments to have been elided. Even for that derivation evidence is provided by location of somatic as well as genital organs in an unnamed glossoscolecoid (Gates, MS) at least two, possibly three, segments in front of the usual positions.

Gonadal conditions in the few remaining microdriles, Aeolosomatidae and Naididae, can be derived theoretically from the ancestral battery by elisions of 4, 6 or 7 segments. For so much excalation no evidence has been found. A different way of bringing naids into a common line of oligochaete descent requires further consideration of the genital conservatism that is basic in the classical system.

The only changes allowed in the gonadal series during the entire period of megadrile evolution are elimination of a pair of testes and/or of one pair of ovaries. The author's studies of parthenogenesis have shown that all reproductive organs, except the clitellum, ovaries and female gonoducts, can disappear in such a short time as to allow no evolutionary changes in specifically distinctive, somatic structure. Although genital evolution presumably is slower in sexually reproducing forms, opportunity for many more than the one or two gonad eliminations of the classical system does seem to have been provided during the Tertiary and Quaternary. Former existence of a longer ancestral series, with gonads at least in segments v-xviii, now is suggested because of the following facts: 1) Location of ovaries in two species of *Haplotaxis* as far back as xv-xvi, gonads formerly in xii-xiv presumably eliminated. 2) Occasional presence in lumbricid individuals of ovaries in some or all of xiv-xviii. 3) Occasional presence of ovaries in xiv of individuals belonging to four other families. 4) Presence of gonad anlage in xii of embryos, various species (3 families) with

no gonads in that segment of adults. 5) Presence of testes in ix of occasional ocnodrilid and microchaetid individuals. 6) Presence of testes in some or all of segments v-ix, all individuals of one common, parthenogenetic morph of *Pheretima anomala* Michaelsen, 1907 (cf. Gates, 1956), of especial interest in connection with the Naididae where testes are in one of segments iv-vii. 7) Gonads in as many as nine segments of head regenerates, several species of *Perionyx*. 8) Gonads in as many as twelve segments of some head regenerates of *Criodrilus lacuum* Hoffmeister 1845.

An ancestral battery of more than eight gonads was suggested by Yamaguchi (1953), but it was characterized only as polytesticulate and without specification as to axial extent.

Presence of supernumerary gonads in unregenerate individuals (one exception, below) is regarded not as a novelty but rather as a reversion to an ancestral condition. That viewpoint seems to be required by the fact that in all sexual megadrile populations reduction rather than extension of gonad series is involved. Indeed, one pair of testes has been lost so recently that the associated but now functionless gonoduct funnels still are present in adults of various species belonging to several families.

Supernumerary gonads in segments produced by halving of mesoblastic somites during early embryonic development (Gates, 1960a) are not cited in support of a longer gonadal series in the megadrile ancestry. Nor was abortion of embryonic somites cited as a method of segment elision. Causation of both anomalies now seems likely to be extrinsic. If, on the contrary, causation can be intrinsic, mechanisms for evolutionary provision of Beddard's intercalations and excalations could be available.

Testes must have been anterior and ovaries must have been posterior in the polygonadal battery now proposed, as such sequence is universal throughout the Oligochaeta. Polygonadal homomorphic head regenerates (*Criodrilus* and *Perionyx* spp.) also have the same order. Even in heteromorphic head regenerates sequence is reversed only with respect to the major axis of the substrate. Anteroposterior axiation of the gonadal battery in the male-female order seems to have been rigidly determined early in oligochaete evolution. Some of the data cited above hint that the first seven pairs of gonads might have been male but in polygonadal batteries of regenerates a variable number of pairs towards the middle of the series often is hermaphroditic. Further specification as to the ancestral battery seems unnecessary because of the mutability of gonad sex already proposed above.

Oligochaete gonads develop on septa from which they usually proliferate posteriorly. The peritoneal covering eventually ruptures releasing gonocytes into the coelomic cavity of the gonad segment or into some partitioned off portion of that cavity. Passage thence to the exterior is by way of ducts opening into cavity of the gonad metamere through a funnel located on the anterior face of a septum and opposite the gonad. Proliferation in the funnel anlage at first is anteriorly and toward the developing gonads but soon is reversed with the result that the ducts grow away from both organs. Moniligastrid testes, the exception to the general rule, proliferate into the interior of their septa. This unique reversal of direction in gonad proliferation, presumably established early in evolution of the family, always is associated with an intraseptal location of the male funnels. Moniligastrid phylogeny, according to the classical system, required an interseptal transfer of male funnels, in case of *Drawida* from the anterior face of 10/11 or a more posterior septum into interior of 9/10. The gonad-funnel association, whether of the moniligastrid sort or otherwise, is so constant even in aberrant individuals as to suggest some sort of causal relationship. If development of either organ is induced by the other the stimulus is more likely to emanate from the gonads and especially since they seem to be the first to appear. Control, then, is effected in the direction of proliferation. Moniligastrid testes though growing into the septum rather than away from it still exert their influence on the nearest susceptible tissue. As a result early proliferation of funnel anlage also is into, instead of away from, the septum but still toward the testis which may even be surrounded at maturity.

Absence of one member of the gonad-funnel association, in the cases hitherto observed, provides no special difficulties. 1) Gonads at testis sites in x and/or xi, funnels lacking. This condition is found in certain male sterile parthenogenetic morphs of various species. Inductive capacity apparently has been lost along with fertility. 2) Ovaries, at testis sites in x and/or xi, funnels lacking. A condition also found in parthenogenetic morphs. These gonads appear to develop more slowly than the ovaries at the usual site in the same animal. Susceptibility to funnel induction may be lost before the inductive influence became effective. 3) Male gonoduct funnels present in x, testes lacking. The anterior funnels often are present in sexually reproducing metandric species and may be continued into more or less normal ducts. The testes, in such cases, abort but only after funnel

development had been induced. Considerable variation in completion of funnel development after initial induction may be associated with differences in time at which the gonad begins to regress.

The octogonadal battery in which gonad nature was irreversibly determined made derivation of microdriles and megadriles from a common ancestor difficult. A polygonadal battery of the sort suggested above permits that derivation economically and by processes now under way or recently completed in extant forms. Gonoduct funnel induction by the gonads, with similar economy, gets moniligastrid funnels into their septa.

Speculation about oligochaete phylogeny, in absence of valid fossil records and in accordance with previously stated assumptions (Gates, 1960b, p. 281), involves estimating comparative stability of organization during long periods of evolution. If structure rather generally shared by extant oligochaetes has not changed uniformly since the Jurassic or Cretaceous⁵ a distant ancestral type may have been characterized somewhat as follows. Body, with homonomous metamerism internally as well as externally. Prostomium, without appendages and simple in comparison with the polychaetes. Setae, no longer in parapodia, in longitudinal ranks of four bundles per segment. Musculature in two layers, the longitudinal internal to the circular of the body wall. Septa, present between all segments. Digestive system, with short buccal cavity, glandular pharynx, simple esophagus and intestine (without special gland diverticula and typhlosoles). Vascular system, with dorsal and ventral trunks connected directly or indirectly in each segment by a pair of commissures. Excretory system, with segmentally paired, simple nephridia each with a preseptal funnel and a postseptal body opening directly to the exterior by a duct in its own segment (presumably ventrally if not close to *B*?). Nervous system, with a simple cerebral ganglion, circumpharyngeal connectives to a subpharyngeal ganglion, a single ventral nerve cord of double origin with a ganglionic widening in each segment, possibly also three pairs of nerves per segment. Hermaphroditic. Gonads, on posterior faces of septa near ventral parietes and nerve cord, as suggested above one pair in each of a number of segments (perhaps 12 or 13), in a continuous series with testes anteriorly.

⁵ Cf. Stephenson, 1930, p. 706. The author has no brief for any of the estimates that have been advanced as to age of the oligochaetes.

Oviducts of most oligochaetes are short, straight, opening directly to the exterior in the segment next behind that containing their funnels. Divergence often is associated with some special condition, e.g., dislocation of septal insertions on the parietes, that obviously is of recent origin. A primitive structure accordingly appears to have been retained rather generally. Male gonoducts of some microdriles are of the same simple kind. Elongated ducts in other oligochaetes usually are associated with special conditions unlikely to have characterized a common ancestral form. Accordingly, all gonoducts of the oligochaete precursor are assumed to have been of the same sort regardless of the gametes they evacuated. All reproductive apertures were minute, superficial, as female pores still are today, and presetal in a middle portion of the ventrum.

Glands of a simple sort, invaginated from the epidermis, are assumed to have been present in the gonad-containing portion of the body. Originally they may have opened into or close beside setal follicles. Some of those "X" glands evolved into various sorts of atria and prostates many of which still develop near setal follicles of the ventrum. Other X glands, judging from the similarity of prostates and spermathecae in certain primitive ocerodrilids, became modified for storage of foreign sperm. In such cases, association with follicles was exchanged for invagination at intersegmental levels.

With appearance of a clitellum (possibly unilayered at first), worms would have been recognizable as oligochaetes. Cocoons now could be secreted for protection of developing young. Sperm could be stored for repeated fertilizations. Profuse production of gametes, in a polychaete manner, no longer was necessary. Henceforth, one of the more important aspects of oligochaete evolution was to be reduction of gamete production and eventually development of more effective means of economic exchange of sperm. The earlier change may not have come about by an immediate elimination of testes and ovaries but rather by establishment of differential rates of maturation throughout the gonad battery. This, at first, may have allowed breeding by each individual to continue through longer periods. As differences in rate of development became more marked some gonads still would be juvenile at death or when breeding was terminated by interposition of unfavorable environmental conditions such as drought. Juvenile gonads would have been associated, just as in various forms today, with functional gonoducts. As a result

of further accentuation of developmental rates, death or termination of breeding would come before funnel and gonoduct development had been induced. Gonads, however, still would have been recognizable as such in early embryonic stages just as those of the twelfth embryonic somite still are in various metagynous earthworms. Eventually, primordial germ cells perhaps would not be aggregated into structures recognizable as definitive gonads even in embryos. Nevertheless, ability to form gonads in sterile segments long was retained. This is demonstrated by occasional presence of juvenile gonads in segments xiv-xviii of certain adult lumbricids as well as by the juvenile testes in v-ix of adults belonging to one parthenogenetic morph of *Pheretima anomala*, a species of a highly specialized and fairly recently evolved genus. In the latter case, the extra testes may be associated with male funnels and even with more or less perfectly developed male gonoducts. Sterilization in the polygonadal battery doubtless proceeded variously. Early in oligochaete evolution, for instance, posterior gonads may have become sterile in lines leading to certain microdrile families while anterior gonads were aborting in a line leading to the Haplotaxidae. Or, in a line or lines leading to other megadriles the change may have affected both ends of the ancestral battery more or less simultaneously.

The number of setae in a bundle also was reduced. Simplification of setal form got under way, finally ending in the sigmoid sort. Before those changes were made, stocks that were to give rise to naid and tubificid families separated off from the main line of evolution. Other stocks that were to become enchytraeid and lumbriculid presumably split off only after trends to simple shape and lumbricin number had gotten well under way. In a line leading to modern megadriles, the four bundles became four pairs of follicles in each of which development is staggered so that only one seta at a time is functional.

An early megadrile probably should be credited with an esophageal gizzard, perhaps in segment v, and two pairs of simple monaxial spermathecae opening by minute and superficial pores in the ventrum at 7/8-8/9.

Any consideration of subsequent evolutionary changes that led to differentiation of most megadrile families must be postponed until much more information becomes available about anatomy and histology of structure that was derogated in the classical phylogenies.

As just hinted, slowly accumulating evidence provides no reason for believing that families and subfamilies can be filiated in straight line sequences in the classical manner. Similarly, the generic filiations of the mother-daughter-granddaughter sort that constituted the more or less esoteric basis of the classical system appear to be improbable when not already known to be impossible. Various classical assumptions such as those of gonad conservatism and irreversibility of sex determination now have been considered and are found to have prevented understanding of evolutionary developments. Restriction of evolutionary importance to a very few pairs of simple characters did of course enable phylogenies of the *Eohippus* to *Equus* sort, but prevented accumulation of data, especially with reference to the circulatory systems, that could have permitted further consideration of megadrile evolution. Variation in gonad location along the anteroposterior axis of extant oligochaetes now can be explained in one or more of several ways, including elimination of gonads at one or the other or both ends of a polygonadal ancestral battery, by change of sex of either sort of gonad though always with retention of the anteroposterior male-female order, by elision of one or two segments at the anterior end of the body in the course of a cephalization process that is common. The classical descriptive terms, holandry and hologyny are inapplicable in certain situations but remain useful only with reference to conditions recently derived from an octogonadal battery with testes in x-xi and ovaries in xi-xii.

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